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ON THE

GERMINATION, DEVELOPMENT, AND FRUCTIFICATION

OF THE

HIGHER CRYPTOGAMIA,

AND

ON THE FRUCTIFICATION OF THE

CONIFERÆ.

BY

DR. WILHELM HOFMEISTER.

55060

TRANSLATED BY

FREDERICK CURREY, M.A., F.R.S., SEC. L.S.

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TRANSLATOR'S PREFACE.

THE work of which the following pages contain a translation has not yet been published in Germany, and a few words are necessary to explain its nature and origin. It is founded mainly upon the author's well-known treatise on the higher Cryptogamia, which appeared at Leipzig in 1851. Since that period Dr. Hofmeister has continued his valuable researches, and the results of his observations have been published in the 4th and 5th volumes of the 'Transactions of the Royal Academy of Saxony,' in the Reports of the same Academy for the year 1854, and in the 'Regensburg Flora' for the same year. In addition to the matter relating to the Cryptogamia, the original treatise also contained some remarks on the fructification of the Coniferæ, and on the analogies between the sexual phenomena in mosses and vascular cryptogams on the one side, and the conifers on the other. Dr. Hofmeister has since published further observations upon this latter subject in the 'Regensburg Flora' for 1854, and in the first volume of 'Pringsheim's Jahrbücher für wissenschaftliche Botanik.'

At the request of the Council of the Ray Society, and

for the purposes of the present translation, Dr. Hofmeister undertook to combine all the above publications into one uniform whole, revising the text throughout, and adding a quantity of matter existing in manuscript, being the results of his subsequent researches. Dr. Hofmeister's object has been to render his work a complete record of all that is at present known of the subjects to which it relates, and the translator feels confident that this object has been fully attained.

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LIBRARY OF THE BOMBAY BRANCH OF THE ROYAL ASIATIC SOCIETY

ON THE

GERMINATION, DEVELOPMENT, AND FRUCTIFICATION OF THE HIGHER CRYPTOGAMIA.

CHAPTER I.

ANTHOCEROS LÆVIS AND PUNCTATUS.

The young germ-plants as well as the adventitious shoots of Anthoceros form linear flat masses of cellular tissue, the breadth of which continually increases from back to front (Pl. I, fig. 1). In the middle of the fore edge a shoot is formed, on both sides of which, in the angles between it and the adjoining parts of the fore edge, new masses of cells are rapidly protruded. These constitute, in the first instance, a vigorous median shoot, on the right and left of which, shoots of a more delicate nature are formed almost contemporaneously, which latter in the progress of growth unite on either side with the median shoot (Pl. I, fig. 7). The new shoots formed by the amalgamation of these actively growing cellular masses unite themselves on either side to the primary shoot, which now constitutes the middle lobe of the fore edge. By the rapid elongation of the new shoots, the primary one increases in breadth, and its original semicircular outline (Pl. I, fig. 7) assumes that of the segment of a circle (2 *b*). In the two indentations of the fore edge of each of the new shoots the same process is repeated, and henceforth the regular ramification of the plant goes on in like manner. At the bottom of the

two indentations exhibited by the fore edge of each shoot (which indentations arise from the amalgamation of three growing masses of cells, viz., a median shoot and two side shoots) three cellular protuberances originate, first a median one, and then two side ones. They grow into one another nearly up to their fore edge, and unite on either side with the median lobe of the fore edge of the next older shoot. By further elongation they become new shoots, producing an increase in the breadth of the median lobe. The ramification of the plant is therefore irregularly dichotomous, depending upon the continual formation of side shoots on either side of a median shoot, which latter is limited in its longitudinal growth — a mode of ramification which, in the case of phænogamous plants, has been called by Schimper "Dichassium." As the new shoots, lying in one plane, diverge from one another at angles exceeding 90°, a succession of three generations of shoots suffices to render the outline of the entire plant circular. The habit of the plant depends, for the most part, upon the extent to which the three component parts of each new shoot amalgamate longitudinally *inter se* and with the median lobe of the fore edge of the next older shoot. Where the elongation of the lower part of the new shoots begins at a late period, there the extent of the amalgamated growth is very considerable. This is the case with specimens of *Anthoceros lævis* growing in sunny open fields. Here, in consequence of the perishing of the oldest shoots, those namely which originate directly from the spore, the plant usually has the appearance of an exactly circular or slightly lobed expansion of dark green, succulent cellular tissue. The extent of amalgamation of the shoots is much smaller in *Anthoceros punctatus*, and still less in plants of *Anthoceros lævis* which have grown in moist shady places or in higher temperature (as, for instance, in pots which have been long under glass). The ramification of Anthoceros is similar to that of the Ricciæ, the Marchantieæ, and several leafless Jungermanniæ, as, for instance, Pellia. In Anthoceros, however, the regularity of the ramification

is much interrupted by the fact that individual marginal cells, and in *Anthoceros punctatus* even the surface cells, become transformed into adventitious shoots. The circumstances under which the plant grows have a decided influence upon the number of the adventitious shoots which come to perfection; and these circumstances also determine whether the growth of such shoots shall terminate at an early period, or whether, like the mother-shoots, they shall continue to ramify and develope themselves. The latter is always the rule in *Anthoceros punctatus*. It contributes much more to the crisped, distorted aspect of the plants of this species, than the perishing of the upper coverings of the air-cavities which are enclosed in their tissue. In *Anthoceros lævis*, ramification only takes place when the plant grows in a very moist atmosphere and in deep shade. Then *A. lævis* ramifies to as great an extent as the other species, from which, however, it is decidedly distinguishable by the entire absence of air-cavities in its tissue.

The flat stem of Anthoceros grows and elongates itself by continual division of the cells of its fore edge. These cells have the form of a three-sided prism, with one side (that, viz., which forms the fore edge) convex. These cells divide repeatedly by septa, which are inclined at angles of about 45° alternately towards the upper and under surfaces of the flat stem. In the cell constituting the fore edge (viz., the cell of the first degree), the division is repeated until the full number of cells belonging to the segment (which segment is limited in its longitudinal growth) is reached. This cell-multiplication terminates at a later period in the median line of the segment than it does at the sides. Hence it follows, that the shape assumed by each of the three lobes of the fore edge of a shoot is that of the segment of a circle. The cells of the second degree, which are distinct from the three-sided prismatic cells of the fore edge, have the form of procumbent prisms with a rhombic base. Each newly formed cell of the second degree divides immediately by a septum parallel to the free outer surface. This division is followed by that of the inner and outer daughter-cells, which takes place by means of a septum parallel to the neighbouring cell, and at right

angles to the free outer surface of the stem (Pl. I, figs. 3, 4). The outer one of the cells thus formed continues to divide by septa parallel to the free outer surface, until the cells have reached the number of which the shoot is destined to consist in the direction of its thickness. This number (about thirteen) is greatest in the median line of the shoot, and diminishes to one at the sides. The arrangement of the cells of a section of the end of a growing shoot, taken through the median line at right angles to the surface, is what is called scalariform; the cells of each longitudinal moiety of the shoot are arranged in rows parallel to one another bearing upwards from the longitudinal axis. Each of the cell-masses which unite to form a shoot consists in its earliest stage of a single cell, situated normally at the bottom of the indentation of the fore edge of an older shoot (Pl. I, fig. 7), but, when destined to form an adventitious shoot, placed at the edge or on the surface of such older shoot. The primary division of this cell, which takes place by a septum inclined to the horizon, is followed immediately by the division of the cells of the first and second degree, by means of a longitudinal septum perpendicular to the surface of the stem. As the young shoot increases in length, the number of its cells, reckoned in the direction of its breadth, increases largely and continually, the cells of its fore edge dividing in like manner by longitudinal septa. Thus it happens that, as long as the shoot grows, its fore edge becomes continually wider. The arrangement of the cells seen from the surface is flabelliform, in rows which radiate from the base of the shoot to the arcuate fore edge. In each of the cells which constitute the permanent upper and under surface of the shoot, four cells are produced by duplicate cell-divisions, which four cells lie in one plane. It follows that, in full-grown shoots, these superficial shells are four times smaller than the internal cells. A suppression of the final septum not unfrequently occurs in individual cells of the inner parenchyma. Some of the latter are often found which are twice the size of the adjoining cells.

The growing cells of the fore edge of young shoots contain a thick coating of a mucilaginous fluid rendered tur-

bid by numerous granules, and in this fluid is a spherical or slightly flattened nucleus formed of a less highly refractive substance (Pl. I, fig. 3). Appearances are not wanting which point to a uniformity in the process of the cell-multiplication with that which usually obtains in the more highly organized plants. The nuclei of the cells of the first and second degree appear sometimes to be undergoing a manifest process of dissolution. Individual cells of the first or second degree are sometimes devoid of nuclei (Pl. I, fig. 3 *). Not unfrequently two nuclei, not separated by any septum, occur in one and the same cell. The wall between the cell of the first degree and the youngest cell of the second degree is always of the greatest delicacy, so as to leave no doubt that it has only just been produced. From these facts it necessarily follows that the vegetative cell-multiplication in Anthoceros (as in nucleate cells generally) commences by the dissolution of the primary nucleus of the cell, which is quickly followed by the formation of two secondary nuclei. Between the two new nuclei a septum is then formed, which extends through the entire cavity of the cell.

In the youngest cell of the second degree, sometimes even in a cell of the first degree, there is produced near the surface of the nucleus a colouring matter consisting of numerous, immeasurably small, coloured particles. The particles are of a pale bluish-green colour in the youngest cells; in the next older cells they tinge the immediate neighbourhood of the nucleus (that is to say, the mass of protoplasm which surrounds it, and from which filaments radiate through the cell-cavity, Pl. I, fig. 3) with a bluish verdigris colour. In rather older cells the colouring matter suddenly seems to be enclosed in a well-defined vesicular body surrounding the nucleus (Pl. I, fig. 6); the somewhat thick, membranous peripheral layer of this body is of an intense emerald green. The less highly refractive substance of the interior of this body is of a much paler colour. At a later period numerous very small starch-granules are usually formed in the interior of the chlorophyll-bodies, and, for the most part, inside the nucleus which they surround. No other changes

* See the lower cell adjoining the apical cell; a cell of the fourth degree.

of importance occur in the chlorophyll-bodies during the life of the cell. Anthoceros alone, therefore, amongst all known plants, exhibits the phenomenon of a single very large chlorophyll-body in each cell.* The form of it in *Anthoceros lævis* is (in most of the cells) globular or ellipsoidal; in the very elongated cells of older shoots it is flattened and spindle-shaped, and then often much drawn out at the points; in the epidermal cells it is much flattened, and, when seen from above, often irregularly stellate. The normal form of the chlorophyll-bodies in *Anthoceros punctatus* is similar. The chlorophyll-bodies of both species are always parietal in the older cells, closely attached to the mucilaginous layer clothing the inner surface of the cell, *i. e.*, the primordial utricle. By treatment with a weak alkaline solution, the primordial utricle shrivels up. It then appears in the form of a delicate sac, to the inner wall of which the chlorophyll-body is attached (Pl. I, fig. 10). In cells which already possess a fully developed chlorophyll-body, the duplication of the latter precedes the division which takes place by the formation of a septum. In cells on the under or upper surface, in which division is about to take place, two separate chlorophyll-bodies are often found, each of which encloses a (secondary) nucleus (Pl. I, fig. 6). In the chlorophyll-bodies of cells which are about to divide, and which bodies occupy about two thirds of the cavity of the cell, the included primary nucleus of the cell always becomes less distinct, and eventually disappears altogether. In the chlorophyll-bodies of other neighbouring cells may be seen two indisputably newly formed nuclei. The chlorophyll-bodies of other cells again exhibit a dark line in the equator of the ellipsoidal chlorophyll-body (Pl. I, fig. 14 *b*), the dark line being the side view of the dense assemblage of immeasurably small coloured particles lying in the equatorial plane. No intermediate stages between this condition and the perfect division of the chlorophyll-body into two parts has been observed; the one seems to follow imme-

* In the 'Vergleichende Untersuchungen,' p. 3, I called this body a chlorophyll-*vesicle*—a name which H. v. Mohl has rightly objected to as inaccurate, inasmuch as, when the chlorophyll-body has swollen and become partly dissolved by the absorption of water, no trace of a surrounding membrane is visible.—'*Bot. Zeitung*,' 1855, p. 107.

diately upon the other. These processes can be seen in the cells of the wall of the lower part of the young fruit whose cell-multiplication is in progress, and still more clearly in the epidermal cells of young shoots. It is true that in the cells of the fruit the chlorophyll-bodies are manifestly smaller than in those of the epidermis. For this reason, however, during the process of cell-multiplication which is constantly going on from above downwards, no doubt can exist as to the mode of succession and the signification of the different states observed. The cells of the upper part of the young fruit contain, without exception, *two* chlorophyll-bodies. It would seem that here an ultimate division of the cells commences, but is not perfected. In the inner tissue of the stem the appearance of two chlorophyll-bodies in one cell is unusual. I once saw between two such chlorophyll-bodies a free nucleus; it was united to both the chlorophyll-bodies by a thread-like filament of granular mucilage (Pl. I, fig. 9).

The position of the organs of fructification of Anthoceros is not confined to any definite points of the flat stem. Both in *Anthoceros lævis* and in *A. punctatus*, groups of archegonia and antheridia are scattered about, apparently without regularity; in some instances occurring in great numbers upon one shoot, in others being very sparingly distributed. The first appearance of antheridia consists in the separation from the underlying tissue of a circular group of about sixteen cells of the upper layer of a very young shoot. Hence arises a small lenticular cavity in the cellular tissue, which is filled with a watery fluid, and only covered by a single layer of cells * (Pl. III, fig. 16). Its basal cells divide by vertical, longitudinal, and transverse septa. Certain of the smaller cells which thus originate (six in number at the utmost in *A. lævis*, but amounting to twenty in *A. punctatus*) grow into short papillæ, which protrude into the intercellular cavity (Pl. III, fig. 16). The dome-shaped portion, which protrudes considerably into the air-cavity, becomes separated by a septum from the primary

* The large cavities in the interior of the cellular tissue of *A. punctatus* are also formed by the separation of cells originally in close cohesion. These usually die-shaped cavities contain at first a watery fluid, and afterwards air.

cell-cavity. In the hemispherical cell which is thus produced there commences, either immediately (Plate III, figs. 16, 17) or after the occurrence of one or two divisions of the same cell by means of horizontal septa, a series of repeated divisions of the apical cell, by means of septa inclined in opposite directions. The cells of the second order which are thus formed are bisected by the growth of radial longitudinal septa (Pl. III, fig. 18). There is thus produced a short clavate mass of cellular tissue, composed of four parallel longitudinal rows of cells. One of the cells of the double pair of cells adjoining its apex divides by a septum which, lying parallel to the longitudinal axis of the organ, forms with the side walls of the mother-cell an angle of 45°. Thus arises an inner cell which is surrounded on all sides by a simple cellular layer. The inner cell expands at the expense of the surrounding cells, the latter becoming tabular and flattened. These cells henceforth multiply only by divisions produced by septa perpendicular to the free outer walls. It is probable that the number of the cells of the cortical tissue of the antheridia increases, but such tissue always consists of a single layer of cells. The inner cell, on the contrary, becomes converted, by means of a series of continued bisections, into a multicellular body, the cells of which become smaller in proportion as their number increases (Pl. III, figs. 19, 20). In its latest stage of development, this cellular body is a spheroidal mass of very small, almost tabular cells (Pl. III, fig. 21). Each of them contains a lenticular vesicle which almost fills the cell. The walls of the cells decay as the antheridia approach maturity. In the mean time, in each of the vesicles, a delicate helicoid filament of from two to three and a half turns, and composed of a substance which is coloured yellowish by iodine (Pl. III, fig. 22), forms itself into an antherozoid. At this period the cellular layer which covers the cavities in the cellular tissue of the frond, and which cavities are almost filled with antheridia, bursts irregularly. It often happens that in the mean time the chlorophyll-bodies have assumed a reddish-yellow colour. The same colour appears regularly and with increased intensity, at the approach of maturity, in the colouring par-

ticles of the cells of the covering layer of the antheridia, of which several, to the amount of eight, are here found in one cell. The antheridia, when fully ripe, open at the apex, the cells of the covering layer parting asunder. The contents, that is to say the lenticular vesicles before mentioned, emerge under water by degrees, and become distributed in the surrounding fluid. The vesicles begin to rotate slowly, during which the enclosed antherozoid becomes free, apparently by the gradual dissolution of the wall of the vesicle. It moves about slowly in the water, rotating slowly round the axis of its spiral.

The formation of the archegonia of Anthoceros differs essentially from that of all other Hepatiæ. A single string of cells, situated on the upper side of a young shoot, and directed obliquely backwards and inwards, becomes filled with granular mucilage. The cells of this row are arranged in a straight line one above another, and form part of a group of cells produced by the multiplication of an upper cell of the second degree. There is no formation of chlorophyll-bodies in these cells (Pl. I, fig. 4). The lowest of the cells of this row swells up during the time that the cells of the stem are increasing in number in the direction of its thickness, and, consequently, before the number of the cells lying between such lowest cell and the upper surface of the stem has reached its limit (Pl. I, fig. 4, *a*). In the basal cell a free daughter-cell is formed, which, increasing rapidly in size, soon fills up the greater part of the mother-cell (Pl. 1, fig. 16). The transverse septa which divide the rest of the cells of the row from one another are then absorbed. Thus there originates a narrow open passage, filled with mucilaginous fluid, which leads into the interior of the tissue of the stem, and into the basal cell of the archegonium, which is now open above (Pl. I, fig. 17). Seen from above, this passage is a hexagonal opening, bounded by six cells of the epidermis, and becoming narrowed inwardly to a cylindrical canal (Pl. I, fig. 18 *b*). By this means the spermatozoa, after their escape from the antheridium, are enabled to reach the immediate neighbourhood of the oval daughter-cell of the basal cell of the archegonium.

So far all the archegonia comport themselves alike. In many, however, the further development now ceases. The daughter-cell which originated in the basal cell disappears. Frequently the walls of the passage leading from the basal cell outwards assume a brown colour. In other archegonia, which in all probability have been impregnated by the entrance of the spermatozoa, the daughter-cell, as well as its nucleus, increases manifestly in size; numerous large granules appear in the fluid in its interior (Pl. I, fig. 17). The oval cell soon divides by an oblique septum (Pl. I, fig. 18), upon which another septum, inclined in a contrary direction, is shortly afterwards seen (Pl. I, fig. 20). In the same manner, the terminal cell divides two or three times by septa inclined in contrary directions (Pl. I, fig. 19). The body, which at this period consists of a few large cells, can now be easily isolated. After some time a division of the apical cell takes place by means of a septum inclined to the ideal longitudinal axis of the organ at the same angle as the previously formed septa, but diverging from them at an angle of 90°, and cutting the under edges of the apical cell. The next septum which is formed stands opposite to this, is inclined in a contrary direction, and forms also a right angle with the two older septa of the cell. The terminal cell of the obtusely conical body, which now plainly constitutes the fruit-rudiment, increases by the production of a series of septa which collectively have the same inclination to the longitudinal axis of the young fruit, but which point in four different directions, and not in two only, as heretofore. The divisions succeed one another in such a manner that the development of a septum turned towards the south is followed by that of another turned towards the north; a septum towards the east is followed by one towards the west, and so on.* The form of the cell of the first degree resembles that of a three-sided prism with one of its long sides turned downwards. The cells of the second degree have partly the form of a parallelopiped, in so far as they originate from the division of the apical cell by

* In the 'Vergleichende Untersuchungen,' an erroneous statement has crept in by a slip of the pen. The series of cell-divisions is erroneously stated to run round the circumference of the apical cell in the course of a right-handed spinal.

a septum cutting one of its sides, and parallel to one of its other sides; and partly the form of a three-sided prism, so far as they originate from the division of the apical cell by a septum parallel to one of its short side-walls. Seen from above, the apical cell has an oblong form (Pl. I, fig. 25); in a longitudinal section, it is triangular if the section is perpendicular to the long side-walls (Pl. I, figs. 21 $^{a, c}$ 23 ^{b}), quadrangular, on the other hand, if the section is at right angles to the shorter side-walls (Pl. I, figs. 21 ^{d} 23 ^{a}). Each cell of the second degree divides, soon after its production, into an inner and an outer cell, by means of a septum parallel to the chord of the arc of the free outer surface. Each of the latter cells is divided by a longitudinal septum radiating from the longitudinal axis of the fruit; those cells adjoining to the side faces of the apical cell being divided at an earlier period, and more repeatedly, than those adjoining the terminal faces (Pl. I, fig. 23). These divisions take place in such a manner that the cell is divided into two portions of unequal size, of which the larger portion immediately divides again by a septum parallel to the septum last formed. Further longitudinal divisions take place (especially in the side cells of the mass of cells which is formed by the multiplication of a single cell of the second degree), in such a manner that, measured in a tangential direction, their number appears to be represented by the odd numbers, 3, 5, 7, &c. (Pl. I, fig. 25). The division of those cells of the outer surface of the fruit which immediately adjoin the apical cell (which division takes place by a radial longitudinal septum) is shortly followed by the formation of a transverse septum, also perpendicular to the free outer surface, but at right angles to the septum just mentioned. In the cells which originate from the smaller cells of the second degeee, the formation of the transverse septum often precedes that of the longitudinal one (Pl. I, fig. 25).

In the rudimentary fruit of Anthoceros, as in other growing organs, one step in the regular series of cell-divisions is often anticipated. It sometimes happens that a division takes place *before* the occurrence of another division which usually follows it, and yet the final arrangement

of the entire mass of cells is not thereby materially affected. The enlargement which takes place in a direction radial to the axis of the fruit, and the cell-multiplication in the direction of the sides of the paraboloid which constitutes the apex of the rudimentary fruit, are somewhat more extensive in the cells derived from the wider cells of the second degree than in those derived from the narrower ones. The outline, as seen from above, of the mass of cells produced by the multiplication of each rectangular combination of four cells of the second degree, which outline is at first elliptical, becomes consequently soon transformed into a circle.

The innermost of the cells into which each cell of the second degree divides is separated by longitudinal septa into two halves. Immediately under the apex, the fruit-rudiment consists of four axial longitudinal rows of cells, which are covered by an almost entirely simple layer of peripheral cells (Pl. I, fig. 24). The fruit-rudiment increases in thickness and circumference by the growth of tangential longitudinal septa in the peripheral cells, which growth is always repeated in the outermost of the new cells, and alternates with the formation in the same cells of radial longitudinal septa. The cells of the base of the very young fruit-rudiment expand considerably in breadth, and thus lay the foundation of the flattened spheroidal enlargement by means of which the fruit is buried in the cellular tissue of the stem (Pl. I, figs. 21 & 22). At the period of the middle age of the fruit, the cells of this swelling not only attach themselves very firmly to the neighbouring cells of the stem, but force themselves inwards between the latter cells to some depth, becoming transformed into cylindrical, crooked papillæ, comporting themselves like short radicular hairs (Pl. II, fig. 5).

The cells of the stem which adjoin the archegonium multiply actively in all three directions of space during the development of the fruit-rudiment. By this means the surrounding tissue keeps pace, for a considerable time, with the increase in size of the fruit-rudiment (Pl. I, fig. 19; Pl. II, fig. 1); afterwards it usually so far outgrows the latter, that a wide hollow space, filled with tough gelatinous

matter, is formed above the young fruit, into which individual cells of the adjoining tissue protrude in the form of jointed hairs (Pl. II, fig. 2). A wart-like elevation of the upper side of the flat stem denotes the spot at which a fruit-rudiment lies concealed within. Owing apparently to the position of the archegonium (*i. e.*, the young fruit), this excrescence is always oblique to the fore edge of the shoot. Eventually the growth of the fruit exceeds that of its covering. One of the causes of this growth is an increase in number (commencing at an early period, and continuing until the bursting of the fruit) of those cells of its lower portion which lie immediately underneath the basal enlargement; or, in other words, a continually repeated division of all the cells of one of the lower zones of cells. Another cause of the growth of the fruit is an expansion of its cells commencing at the apex of the fruit at the period when the apical cell ceases to multiply, and extending slowly to the base (Pl. II, fig. 5). The fruit breaks through the arcuate lid of the surrounding cavity, and carries the decaying tissue of the lid upwards, attached to the gelatinous mass which is accumulated above the apex of the fruit, and which is traversed by the jointed hairs now broken up into their individual cells; it (the fruit) then appears above the surface of the stem, apparently surrounded by a sheath. The dome-shaped mass of gelatine, covered with a brownish layer of cells, is the so-called Calyptra of the earlier observers (Pl. II, figs. 4, 5 *b*). The differentiation of the parts of the internal tissue of the fruit begins shortly before the latter breaks through its covering, and proceeds from above downwards. Certain cells, forming an axile cylindrical string of from twelve to sixteen rows of cells, one above another (each now showing four cells in transverse section), cease to form horizontal septa, whilst in all the other cells at least one more such division takes place (Pl. II, fig. 5). This string of cells is the future columella. The layer of cells immediately surrounding it is that out of which the spores and elaters are developed, which extend from the columella to the wall of the fruit. In this layer the multiplication of the cells by division by horizontal septa is twice as active as

in other parts of the fruit. Measured vertically, one cell of the columella, or two of the wall of the fruit, are equal to at least four of the cells of the latter layer (Pl. III, fig. 1). The wall of the fruit is thinnest in its upper part. It consists there of only four layers of cells, whilst towards the base there are five such layers (Pl. III, fig. 1), being the result of the division of the cells of the second layer (reckoning from without inwards) by longitudinal septa parallel to the longitudinal axis of the fruit.

Those cells of the layer surrounding the columella which are destined to be the mother-cells of spores become detached from the neighbouring cells, and assume a spherical form. Their contents consist of finely granular protoplasm, and a large central transparent nucleus with a large nucleolus (Pl. III, figs. 1, 3). Those destined to form elaters remain less developed. Their nucleus disappears; in its place are seen two new nuclei, between which a septum is produced, dividing the cell into two daughter-cells (Pl. III, fig. 1 *b*). The same process recurs in one, sometimes in both, of the newly formed cells; so that the fully grown elater consists of a row of three or four cells.

The perfecting of the spore-mother-cells proceeds slowly from the upper to the lower part of the fruit. A well-made longitudinal section of a half-ripe fruit exhibits a graduated series of all the different states, from the first separation from the neighbouring cells up to the formation of the spores. The spore-mother-cell increases rapidly in size after becoming detached from the neighbouring tissue. The protoplasm in its interior divides into strings, radiating from the nucleus, and into a thin parietal layer (Pl. III, fig. 4). Shortly afterwards an accumulation of mucilaginous plasma is formed close to the primary nucleus which occupies the middle point of the cell. This plasma, in *Anthoceros lævis*, is usually coloured green by the particles dispersed in it; in *A. punctatus* it is colourless. This accumulation divides itself into two halves, each of which clothes one of the poles of the globular nucleus (Pl. III, figs. 5, 5 *b*). In slightly older cells, two newly formed secondary nuclei are found near the primary nucleus, surrounded by a halo of finely granular protoplasm, from which strings

of protoplasm radiate to the inner wall of the cell (Pl. III, fig. 6). The new nuclei, in *Anthoceros lævis*, usually consist of a greenish substance; in *A. punctatus*, of a colourless substance, containing coarser particles. They doubtless originate from the fact, that each of the accumulations of protoplasm which clothe either pole of the primary nucleus, has become rolled into a ball, and distinctly defined. The layer of protoplasm which surrounds each of the newly formed nuclei, often contains so many granules, that the outlines of the latter are at first completely concealed, and only become visible long after their first production. The contrary, however, is frequently the case in both species. The secondary nuclei are often without any solid substances in their interior. Sometimes they contain a single large nucleolus; sometimes a larger number of granules, which, becoming blue with iodine, indicate the existence of starch. Late in the autumn, after the occurrence of the first frosts, each of the secondary nuclei is found, in many of the fruits, surrounded by a thin-walled, rather larger cell (Pl. III, fig. 15). Fruits of this kind decay without further development: their state is one of disease.

In more fully developed mother-cells lying nearer to the apex of the fruit, the outlines of the secondary nuclei are hazy and less defined. Ultimately two masses of granular protoplasm are found occupying their place, the limits of which are confluent with the surrounding layer of protoplasm (Pl. III, figs. 7, 8). In the mother-cells immediately above, each of these masses is divided into two sharply defined globular balls, *i. e.*, into two tertiary nuclei. Their position at first is ordinarily decussate (Pl. III, fig. 9); at a later period, they usually group themselves in a manner answering to the four corners of a tetrahedron. They are bound together by thick strings of protoplasm; thinner strings of more finely granular, almost transparent protoplasm proceed in greater or less numbers from each nucleus to the inner wall of the cells (Pl. III, fig. 10). Up to this point the primary nucleus of the cell has become continually more transparent and paler; now, it and its nucleolus have disappeared. Immediately thereupon the mother-cell divides into four daughter-cells; the special-mother-cells,

by means of six triangular septa, passing between each two nuclei, and cutting each other in the middle point of the cell. The wall of the mother-cell increases manifestly in thickness from the time of the appearance of the secondary nuclei until the formation of the septa. In *Anthoceros lævis*, it remains smooth; in *Anthoceros punctatus* it is furnished with numerous dots (*Tüpfeln*); (Pl. III, fig. 23). The inner layers of the thickened wall are very sensitive to the action of water, especially in *Anthoceros lævis;* they swell up rapidly, and to a great extent, contracting the cavity of the cell, and compressing its contents into a small space, causing great difficulties to the observer. The affinity of the swelling layers for water is so remarkable, that the swelling takes place even in saturated saline solutions. Alcohol is the only medium in which it fails to occur; it is very much diminished in diluted alcohol. If spore-mother-cells, in which the four tertiary nuclei are fully formed, are placed in diluted alcohol, the cell-contents first contract; a slight swelling of the membrane of the cell then begins, which increases in proportion as the alcohol escapes by evaporation from the fluid. It is now plainly seen that it is one of the middle layers in particular of the cell-wall which increases in size by absorption of water (Pl. III, fig. 11). The outermost layer of the membrane passively follows the increase in size of the middle one, and becomes expanded. If pure alcohol is added, water is withdrawn from the swollen membranous layer; the latter diminishes in size; the outer layer of the cell-wall thereupon becomes wrinkled, inasmuch as its volume does not diminish in the same proportion as that of the middle layer, and its elasticity does not equal its power of expansion. H. v. Mohl has shown that the formation of the septa of the mother-cells progresses gradually from the periphery to the centre; and he has figured a condition in which this growth has taken place to so small an extent that the yet imperfect septa have not interfered with the strings of protoplasm uniting the four tertiary nuclei.* The rapid swelling up of the walls of the mother-cells prevented me for a long time from repeating this observation, which

* 'Linnæa,' 1836; "Vermischte Schriften," tab. iv, fig. 23.

is certainly of great importance with reference to cell-multiplication. However, since I made the experiment of using alcohol in the observation, I found in every fruit which was submitted to dissection spore-mother-cells (situated between spore-mother-cells which were yet undivided and others which were already completely divided into four daughter-cells) the inner walls of which were traversed by the rudiments of the future septa, in the form of ridges protruding inwards (Pl. II, fig. 12). By adding water to such a preparation, the imperfect septa are seen to be direct continuations of the innermost layer of the cell-wall, which layer swells up but little in water (Pl. III, fig. 13). The swelling up of the inner layers of the membrane of the mother-cells has a peculiar appearance in those mother-cells in which very numerous strings of protoplasm pass from the tertiary nuclei to the cell-wall. The enlarging substance of the membrane does not force these strings inwards, but shapes them to itself and clings to them (Pl. III, fig. 15). The swollen substance of the membrane is manifestly less firm than that of the strings of protoplasm.* Nevertheless, the swollen layer of the wall exhibits sharp broken edges when the cell is ruptured by pressure with the covering-glass. It is only after prolonged soaking in water that the substance of the swollen layers becomes disintegrated; the middle layers first dissolve, and then the innermost ones; the outermost layer remains behind to the last.

After the walls of the special mother-cells have attained a moderate thickness, there is formed in each one of them a single spore, which, from the first moment of its membrane becoming visible, occupies the entire cavity of the mother-cell. In *Anthoceros punctatus*, the prominences attached to the outer membrane of the spore exactly fill up the dots of the wall of the mother-cell. Irregularities of spore formation occur in both species: occasionally two special-mother-

* It was probably the observation of similar cases which led Kützing to the erroneous notion that the prolongations of the exosporium were hardened, thread-like prolongations of the protoplasm surrounding each of the nuclei. ('Philos. Bot.,' Leipz., 1851, p. 264.) The error of this view is at once manifest, from the fact that the exosporium of Anthoceros presents, at its first appearance, an entirely smooth outer surface. Its protuberances originate at a later period.

cells and two spores only are formed in some of the mother-cells, in which case the two spores are double the usual size; this is similar to what occasionally takes place in the formation of the pollen of many phænogams. When the upper four-fifth parts of the long cylindrical fruit have become filled with ripe spores, the wall, which assumes a dark brown colour as soon as it contains ripe spores, splits longitudinally into two halves, and the spores which have become free by the absorption of the walls of the mother-cells are dispersed. These spores are of a brownish-yellow colour in *Anthoceros lævis*, and somewhat darker in *Anthoceros punctatus*.

Both species are also reproduced by buds. These are formed in the interior of the tissue of the stem in the following manner:—The contents of individual cells of that tissue, after a slight contraction of the entire upper surface, become clothed with a new membrane (Pl. I, fig. 11), and the new cell thus formed becomes transformed into a cellular body by a series of divisions following the course of those which occur in the cell-multiplication of young shoots (Pl. I, figs. 12, 17). This cellular body sometimes commences its own independent development by the protrusion of radicular hairs, even whilst fully enclosed in the cellular tissue (Pl. I, fig. 13). The contents of the cells of very young buds consist of colourless protoplasm; the cells of older buds are filled with numberless small starch-granules, between which is seen a dark bluish-green colouring matter, composed of extremely minute particles. The buds are usually set free by the disintegration of the tissue surrounding them, which takes place as the stem slowly decays from back to front. If they remain very long enclosed in the tissue of the stem, a discoloration of the parenchyma commences in their middle, which is followed by the breaking up of the bud into its component cells, and this latter process advancing gradually to the periphery ultimately destroys the bud. The development of the spores of Anthoceros is a process which has been the subject of very many observations (Mohl. sup. 'Nägeli Zeitschr. f. Botanik,' H. 2; Schacht, 'Berl. Bot. Zeit.,' 1850, 24—26). The observers just cited agree with me as to the

facts observed in all essential points; but there is a difference of opinion as to the interpretation of these facts. Mohl assumes that the duplication of the secondary nuclei takes place by gradual constriction;* Nägeli, that it occurs by the growth of a septum bisecting the internal cavity of the secondary nucleus of the first order, and by the subsequent differentiation of the two halves; Schacht's notion of the process approximates to that of Mohl, from which my own explanation only differs in the mode of expression.

Figures of Anthoceros are to be found in Dillenius ('Historia Muscorum,' tom. lxviii, figs. 1, 2), in Schmidel ('Icones pl.,' t. xix, *A. lævis;* t. xlvii, *A. punctatus*), and also in Hedwig (*A. lævis*, theoria generat., ed. ii, t. xxix, xxx). According to these figures, the characters of the flowers appear to be principally grounded upon a "radiating mode of growth, progressing in all directions from a central point of attachment." The history of the development of the fruit which is given by the above observers does not extend further back than the appearance of the fruit above the edge of its veil or covering. Nees v. Esenbeck ('Naturgeschichte der Europ. Lebermoose,' B. iv, s. 334, 1838) describes the rudiments of the fruit, whilst enclosed in the substance of the stem, as archegonia (*Stempel*). Bischoff, on the other hand, had already (1835) rightly described the relation of the young fruit to the tissue of the stem which covers and encloses it ('Nova Acta Acad. C. Carol. Leop.', T. xvii, p. 2, s. 934), and has figured it. ('Handb. der Botan. Terminol,' B. ii, t. lxvi, fig. 2783.) He does not mention the archegonia. Schacht has lately ('Berliner Bot. Zeit. Jahrg,' viii, 1850, N. 24—26) published a contribution to the history of the development of the fruit and spore of Anthoceros. My own observations, in the 'Vergleichende Untersuchungen,' were completed before the appearance of Schacht's paper. Schacht has only once observed an archegonium (l. c. 459), unfortunately an imperfect one, of which the essential parts were already decayed. The arrangement of the cells of the stem adjoining the base of the archegonium appeared to him to bear a great

* See Wagner's 'Handwörterbuch der Physiologie,' Bd. iv, s. 215.

resemblance to that occurring at the base of the rudimentary fruit. This led him to the erroneous conclusion, that the fruit was the product "*of certain cells lying at the bottom of a small, narrow, deep canal of the leaf.*" The above remarks show the inaccuracy of this view. The following observations will exhibit the essential agreement in fruit-formation existing between Anthoceros and the liverworts and mosses generally.

CHAPTER II.

LEAFLESS JUNGERMANNIÆ.

Pellia epiphylla, Aneura pinguis and multifida, Metzgeria furcata.)

Amongst all the liverworts indigenous to Germany, *Pellia epiphylla* has the largest spores. They are oval, surrounded by a delicate, finely granular outer membrane; in the ripe state, as they escape from the opening fruit, they are multicellular. They usually consist of four cells, arranged in a single row, two of which are disc-shaped and two hemispherical (Pl. IV, fig. 1). Sometimes one of the former is divided by a longitudinal septum, so that the spore is 5-cellular (Pl. IV, fig. 2). The internal cavity of the cell contains much chlorophyll; the green of which, appearing through the thin, pale-yellowish wall of the capsule, imparts to the unopened fruit its dark colour. The cell which constitutes one of the ends of the spore contains a far smaller quantity of chlorophyll-granules than the other cells. From it springs the first of the long root-like papillæ by which the plant is attached to its place of support. The cell next to this divides by a longitudinal septum a few hours after the spores have been sown on moist earth, even if such division has not taken place earlier; the same process then follows in the neighbouring cell, and frequently also in the cell opposite to the radicular cell. Each pair of cells of the middle region of the germinating spore is doubled by longitudinal division, taking place principally in the direction of one of the transverse diameters (of the spore). Some varieties occur throughout the whole extent of the cell-multiplication caused by this longitudinal division, which, however, have little influence upon the ultimate form of the plant. The division begins in the cells next to the rooting cell (Pl. IV, fig. 3), sometimes

only in one of these cells (Pl. IV, figs. 4, 5, 9), sometimes in the cells next but one to the rooting cell (Pl. 4, figs. 6, 7), or even in one only of such cells. The germ-plant consists now of the basal cell, which is protruding the first radicular papilla; of two sets of cells above the basal cell, each consisting of from two to four cells adjoining one another; and of the apical cell, which is already not unfrequently divided by a longitudinal septum (Pl. IV, figs. 9, 10).

The activity of cell-multiplication in the direction of the breadth of the plant increases continually towards the apex. Although it never occurs more than once in the cells next to the basal cell, it is a rare occurrence when it only takes place in *one* of the next higher cells, and it is a rule almost without exception that it happens repeatedly in the fourth pair of cells reckoned from the basal cell upwards (Pl. IV, figs. 12, 14). Hence the plant assumes the form (more and more distinctly marked as it advances in growth) of a plate widening continually towards the fore edge. In its earliest youth the base, notwithstanding the smaller number of its cells, is as wide or wider than the apex. The expansion of the lower cells, which occurs at an early period, keeps pace up to a certain point with the increase in breadth of the upper cells. But, when a month old, the outline of the young plant has already assumed the shape of a spatula (Pl. IV, fig. 14).

The expansion of the cells adjoining the base of the plant begins at the time of the protrusion by the basal cell of the first rootlet; this takes place contemporaneously with the commencement of the multiplication of the cells in the direction of the longitudinal axis, which latter results only from the continual division of the apical cell, or (as is more often the case) of the two adjoining apical cells. Both cells divide contemporaneously by a very oblique* longitudinal septum, upon which a similar septum, inclined more obliquely, but in the opposite direction, is soon imposed (Pl. IV, figs. 7, 8, 13). This division of the terminal cells by septa alternately inclined in different directions to the surfaces of the plant, is repeated continually, and with tolerable rapidity; for instance, twice in

* The longitudinal axis of the spore being considered to be vertical.

three days in a plant kept moist upon the stage of the microscope. If the number of the apical cells of the plant increases in a lateral direction by the division of the existing cells, the like process immediately follows in all the newly formed cells: in the entire row of apical cells division takes place continually by septa inclined either to the upper or the under surface of the plant. The newly formed cells of the second order divide, very shortly afterwards, by septa almost parallel to the surfaces of the plant (Pl. IV, fig. 13). By this means the number of layers of cells increases, and with it the thickness of the plant. This increase is only slight at first; it does not seem that the process is repeated whilst the plant is quite young, or that either longitudinal or transverse sections exhibit more than four layers of cells. Very frequently those cells only divide which are turned towards one (? the lower) surface; the plant then consists, in the direction of its thickness, of three layers of cells (Pl. IV, fig. 16). By this time certain of the superficial cells of the plant are divided once or twice by a septum perpendicular to the surface, which cells consequently appear twice or three times as small as those in the interior of the tissue (Pl. IV, fig. 13). This is afterwards the normal condition. By the penetration of the first rootlets into the ground, the young plant is set erect. It retains this position only a short time. The expansion which immediately commences in the the cells of its lower portion is not uniform; the cells of one surface expand far less in a longitudinal direction than those of the other (Pl. IV, fig. 13): hence it follows, that the apex of the plant becomes more and more inclined towards the less expanded side of the basal cell, *i. e.*, the future under surface of the plant; so that the direction of the growth of the young Pellia is parallel to the surface of the soil beneath it. Individual cells of the under side, especially those lying in the median line, grow out into long rootlets, which penetrate deeply into the ground. The rootlets originate in the following manner: at a certain point, usually, exactly in the middle of the outer surface of one of these cells, the membrane grows out into a strongly developed point, which shortly leads to the formation of a

long tube attached to the cell. The mode of origin of the first main root does not differ essentially from that just described; the conical cell which emits the rootlet usually (not always, see Pl. IV, fig. 12) becomes transformed by degrees into the main root.

In consequence of the commencement of the expansion of the basal cell of the germ-plant, the outer membrane of the spore (which, although it has become considerably expanded and more delicate, has, nevertheless, up to this point, still enclosed the germinating spore) is ruptured (Pl. IV, fig. 10). The *débris* of this membrane may be found, for some time afterwards, attached to the apex of the young plant (Pl. IV, fig. 13).

By this time, the cells nearest to the fore edge of the young Pellia have begun to protrude short club-shaped hairs (Pl. IV, figs. 13, 14), which appear in increased numbers as the growth of the plant progresses (Pl. IV, figs. 24, 27).

From six to eight weeks after the sowing of the spores, the germ-plant has, partly by the multiplication and partly by the expansion of its cells, attained a length of from $\frac{1}{3}'''$ to $\frac{2}{3}'''$. It is now attached to the ground by a larger number of rootlets; the fore edge, from repeated division of its marginal cells, has become wider than the older parts. At every repetition of a longitudinal division of the marginal cells, the septa, which continue to be perpendicular to the surfaces of the plant, appear to diverge laterally more and more in the fore part of the plant. The consequence is, that the arrangement of the cells (Pl. IV, fig. 15) is flabelliform. The sides of the fore edge grow more rapidly than its middle, partly on account of a more frequent division of the cells by means of septa inclined alternately in different directions, but principally on account of a more vigorous expansion of the cells. The apex of the young plant appears indented, at first slightly, afterwards more deeply (Pl. IV, fig. 15). The cell which occupies the bottom of the indentation begins all of a sudden to multiply itself actively. It divides twice by a transverse septum perpendicular to the surfaces of the plant. The foremost of the new cells divides by a longitudinal septum into two, each of which is again divided

by a transverse septum. The body thus formed, of which the ground plan exhibits five cells, now protrudes into the indentation of the fore edge (Pl. IV, fig. 17). The further multiplication of its cells in the superficial direction takes place, in the following manner: a membrane, directed obliquely outwards, is mounted upon each of the last-formed transverse septa; thereupon each of the inner ones of the four newly formed cells of the fore edge divides by a transverse septum at right angles to the longitudinal axis of the shoot. In each of the outer cells there is formed, at the same time, a longitudinal septum parallel to the last-formed oblique septum. By this means the ground is laid for the fan-shaped arrangement of the cells of the middle shoot.

All that is now necessary for the development of the cell-arrangement of the half-developed (Pl. IV, fig. 23) as well as of the perfect middle shoot, is the repetition of the division by transverse septa of the two middle cells of the fore edge—the repeated transverse division of the cells laterally adjoining the latter—the commencement of a longitudinal division in these cells after a repetition once or twice of the transverse division, and lastly,—the frequent recurrence of the same series of divisions in the lateral cells for the time being of the fore edge of the shoot.

The growth of the middle shoot of the germ-plant is limited, as is the case with all the divisions of the stem in Pellia. The multiplication of its lateral cells is slight at the base, increases to the middle, and increases rapidly from thence to the apex. The form of the shoot is therefore either that of a short spatula, or semi-oval.

The cells which are situated in the axil formed by the middle shoot and the lateral wing of the germ-plant begin to multiply vigorously, according to a similar rule, as soon as that shoot has attained to about a fifth part of its development. The cell, which, when seen in profile or from above or below, is oblong or trapezoid, appears, when viewed in the direction of the surface of the plant, divided in the first instance, by means of a transverse septum, into two cells, of which the hinder cell is square, and the front cell trapezoid. The latter divides by a longitudinal septum; each of the newly formed ones again by a transverse septum; the outer

cells thus formed divide by laterally inclined longitudinal septa, and so on, as in the case of the origin of the middle shoot. The like process is repeated in the angles at both sides of the new shoot, soon after the commencement of its formation. A shoot originates in each angle, which unites in growth with the median shoot, on the side which is turned towards the latter. By this means a new shoot is formed on each side of the middle segment of the fore edge of the young plant (Pl. IV, fig. 19), which new shoot, in consequence of its being composed of three united shoots, is tripartite at its fore edge. The flat cellular masses which thus originate unite in growth firmly and intimately with the middle shoot, by the edge which is turned towards the latter. The new shoots, composed of these amalgamated cellular bodies, protrude from the indentations of the fore edge of the young plant, in consequence of the commencement of longitudinal expansion in its basal cells; by their expansion, the middle lamellæ which are united to them are drawn out laterally. Their form is now a complete repetition of that of the germ-plant in its earliest stage: the fore edge exhibits a short, spatula-shaped median segment, and two lateral wing-shaped ones. The subsequent ramification takes place in like manner. There is one invariable rule for the entire development of the plant, commencing from the formation of the middle shoot of the germ-plant: the rule is, that each shoot has its origin in the amalgamation of three shoots, which are formed almost contemporaneously in one of the indentations of the fore edge of an older shoot. Each new shoot, therefore, exhibits at its first appearance two indentations of the fore edge. According to the ordinary rule, new shoots are formed only in those indentations which point out the boundaries of the three amalgamated shoots. Hence arises the furcate ramification of the plant (Pl. IV, figs. 19—22). The growth of each shoot is limited.*

* Bischoff considers that the first shoot of the germ-plant of Pellia is a prothallium, distinct from the subsequent shoots. ('Handb. d. Terminologie,' ii, 733; 'Botan. Zeitung,' 1853, 115.) As, however, the first shoot is not distinguishable in any essential particulars from the later ones, I agree with Gottsche ('Bot. Zeitung,' 1858, Anhang, 16) in thinking that there is no ground for this distinction.

The multiplication of the cells of each shoot in the direction of its longitudinal axis takes place exclusively in the cells of the fore edge. In the young germ-plant they divide, as has been shown above, by septa inclined to the horizon alternately in different directions. The form of the cell-multiplication in the fore edge of the growing shoots of older plants is essentially different. Here the marginal cells divide by septa which are parallel to one another, slightly convex on the inner side, and perpendicular to the surfaces of the plant. This form of division often occurs in young germ-plants of two months old (Pl. IV, fig. 24). The phenomenon which occurs so frequently,—viz., the fact that in the earliest stages of development the division by horizontal septa parallel to one another* precedes that which in all subsequent stages is the normal mode of cell-multiplication, viz., division of the terminal cell by septa alternately inclined in different directions,—makes it probable that the latter form of cell division is to be looked upon as a more perfect, higher form of growth than the former. Still more remarkable is the fact (which as yet stands alone), that in Pellia the simple, apparently lower form of cell-multiplication follows, in point of time, the more complex form which occurs in the later periods of the life of the plant.

This phenomenon appears most distinctly in the first spring-shoots of fruiting specimens. Here the cells of the fore edge of the first, second, and third order exhibit, during the growth of the shoot, large and manifest nuclei, from which mucilaginous threads often pass to the walls of the cells; they contain, besides, a slightly granular, yellowish slime. In the older cells lying behind the fore edge, numerous small chlocophyll-granules make their appearance; the nuclei of these cells are less easily seen (Pl. IV, fig. 25). The cell of the first order—the terminal cell—has the form of a slice taken from the middle of a double convex lens by two sections parallel to the small axis; the cell of the second order, at its first appearance, is shaped like a

* This occurs in the prothallium of mosses, in the suspensor of Selaginella, in the greater number of phænogans, and in the rudiments of the fruit of many mosses.

similar slice from a Meniscus. Through the division of these cells by means of septa parallel to the surfaces of the plant, the shoot increases in thickness. The first of these septa does not coincide with the ideal axis of the shoot; the two parts into which it divides the cell are very unequal (Pl. IV, fig. 25). The two newly formed cells divide again several times by horizontal septa; the thickness of the plant, however, never seems to go beyond eight layers of cells. From some of the cells near the fore edge, hairs, shaped like a club, and bent forwards, take their origin. The latter become bicellular, soon after their appearance, by the growth of a transverse septum. The basal cell, when fully grown, usually contains starch-granules; the terminal one, a thin fluid mucilage. A membranous layer of tough gelatine encloses the growing fore edge of these hairs. The cells which form the permanent upper and under surface of Pellia ultimately divide by a vertical, longitudinal, and transverse septum; so that each cell of the outer layer is four times as small as one of the neighbouring inner cells. This division occurs sometimes in the fourth youngest, sometimes even in the seventh youngest group of cells produced by a cell of the second order. As the growth of a shoot progresses, the activity of the cell-multiplication in the direction of its thickness diminishes continually from the base to the fore edge, more slowly, however, in the median line than at the sides. The free margin of each shoot of which the development is completed, is formed of a single layer of cells; at the base of the indentations of this margin are found protuberances of cellular tissue projecting downwards: these are the young new shoots.

The shoots of barren plants growing in flowing water exhibit conditions in the position and shape of their cells, which can only be explained by looking upon them as forms transitional between the first and the second form of cell-multiplication (Pl. IV, figs. 26, 27).

It is a remarkable circumstance that, in the earliest spring-shoots of Pellia, the two sides, owing to the more vigorous expansion of the cells of one of them, are always unequally developed. One of the shoots which protrude themselves from the indentations of the fore edge pushes

up apparently to the apex of the parent shoot through the distortion of the outline of the latter, whilst the other appears at some depth below, closely pressed to the side (Pl. IV, figs. 20, 21). The former is always developed more rapidly than the latter (Pl. IV, fig. 22), which often fails altogether, often remains quiescent for months and then suddenly begins to grow. Most of the disturbances of the regular furcate ramification have their origin in the circumstances just mentioned.

It is only in barren plants (where it often occurs) that shoots are found on the upper side also of the flat stem. In individual cells of the surface there commences a process of cell-multiplication differing, so far as regards its regular mode of progression, in no material respects from that which obtains in the germination of spores (Pl. IV, fig. 28). A number of shoots of the above nature, similar to germ-plants, only more fleshy, are often situated close together:—in old joints of the stem I have counted as many as thirty upon a single joint. The tufted mode of growth of barren Pelliæ in flowing water may, perhaps, be owing to these shoots.

On the upper side of the earliest spring-shoots of fertile Pelliæ, club-shaped cellular masses are protruded, consisting of a short central string, usually of only two cells, surrounded by a single layer of four cells, each lying at the same elevation (Pl. IV, fig. 29): these are the first rudiments of the antheridia. The arrangement of the cells leads to the conclusion that they have originated in the division by means of septa inclined alternately in different directions, of one of the cells of the upper surface. Each cell of the second order is divided by a longitudinal septum; two of the cells thus formed, which are placed one above another, and have almost the form of the quadrant of a cylinder, are divided by a septum cutting the side-walls at an angle of 45°, into an inner three-sided and an outer four-sided cell, of which the latter has an arched outer surface. This determines the structure of the first rudiments of the antheridium. By continual multiplication of the five cells of its clavate end, the inner one of which divides in all three directions, the four outer ones only in the direction

of the tangent, the antheridium assumes the form of a mass of cellular tissue, supported upon a very short stalk, consisting of four cells. Contemporaneously with the first appearance of the young antheridium above the surface of the joint of the stem, an annular wall of cellular tissue is raised round the antheridium by means of repeated division of the adjoining cells of the upper surface of the frond (Pl. IV, fig. 29), which wall, keeping pace in its growth with that of the antheridium, surrounds it when ripe, enclosing an open space above its apex.

The cells, sixteen to twenty-five in number, of the outer cellular layer of the ripening antheridium are flattened and tabular (Pl. IV, fig. 30). Their walls are covered with rather large chlorophyll-bodies (starch-grains surrounded by a very thin green layer), which, when the organ is fully ripe, assume a dull yellow colour. The inner cells continue to divide for a long period by alternate longitudinal and transverse septa; so that the antheridium, when nearly ripe, consists of a globular mass of very small, four-sided, tabular cells, surrounded by a single layer of large, flat cells, containing chlorophyll. Each of the small tessellated cells contains a lenticular vesicle, in which a spiral thread is formed, consisting of transparent mucilaginous matter (Pl. IV, figs. 30—32). When the antheridium is fully ripe, the cells of the covering layer separate from one another at the apex; the small cells, whose primary intimate adhesion has been destroyed by the softening and swelling up of the cell-membranes, escape through the crevices, mixed with mucilaginous granules, in the form of a thick pultaceous mass; when brought under water, they disperse themselves in the fluid. The spiral thread enclosed within them (the spermatozoid) soon exhibits an active whirling motion, in consequence of which it resembles a closely wound watch-spring (Pl. IV, fig. 32 $^{a, b}$); it is still surrounded by the lenticular vesicle, which, however, during the motion, can with difficulty be seen. When the wall of the vesicle which envelopes the spermatozoid bursts (which usually occurs after the vesicle has been in the water for half an hour), the spermatozoid immediately escapes through the fissure. It then forces its way through the gelatinous, softened substance of the wall of the

(originally tabular) mother-cell. The turns of the spiral are drawn out from one another, so that it assumes the form of a screw. The spermatozoid moves about with some rapidity in the water, keeping up a continual revolution round its own axis, and often dragging behind it the ruptured vesicle. The hinder end of the spermatozoid is drawn out into a very long, fine point; the opposite end is thickened, but hardly perceptibly so. At this end I saw very clearly, in spermatozoids whose motion had been arrested by a solution of iodide of potash, two long, thin, lateral cilia, exactly like those which Thuret discovered in the spermatozoa of Chara. The observation of these cilia, which I could not succeed in finding in any other liverwort, is a matter of some difficulty even in Pellia with our present magnifying powers. The cilia, and the thread-shaped ends of the spermatozoa, which sometimes adhere to other bodies, exhibit an active motion which is winding and helicoid rather than pendulous. One end of a spermatozoid will often remain attached to the mucilaginous mass which escapes with it from the ripe antheridium. The movements of the spermatozoa last only a short time; ten minutes after their escape they relax sensibly; in all the cases which I have observed, they have ceased entirely after two hours and a half.*

The number of the antheridia is very large; it often amounts to fifty on the same shoot. They first open at the beginning of May; but even at the end of June a good number of ripe ones may still be found. Upon Pelliæ growing in running water, which, as a rule, are barren, isolated antheridia are not unfrequently found; but archegonia are hardly ever met with.

Upon the shoots situated in the indentations of the fore edge of those spring-shoots which bear antheridia, oval, closely packed cellular bodies are protruded, varying in number from four to twelve; these are the first rudiments of the archegonia. Immediately after their appearance, the young shoot makes a further growth underneath them, but without attaining to

* Thuret has shown that spermatozoa of a like structure exist in all the Muscineæ. ('Ann. Sc. Nat.,' 3rd ser., vol. xvi). He has given very good figures of those of Pellia (l. c., pl. x). Schacht's figures ('Die Pflanzenzelle,' Berlin, 1852, pl. v) do not exhibit correctly the relation of the cilia to the body of the spermatozoid.

the same thickness as before. The archegonia, consequently, appear to be seated upon the scarp produced on the upper surface by the sudden diminution in thickness of the joint of the stem (Pl. V, fig. 1). The development and structure of their first rudiments correspond exactly to those of the very young antheridia. A cell of the upper surface of the yet very young shoot becomes slightly arched outwards; it divides by a septum inclined to the surface of the stem, and the upper one of the newly formed cells divides by a septum inclined in an opposite direction to the latter septum. Whilst the division is repeated in the new terminal cell by a septum perpendicular to the last and parallel to the last but one, the last formed joint-cell divides by a vertical septum into two cells whose basal outline is a quadrant. The same process recurs in each second-youngest cell, whilst the terminal cell divides anew by a septum inclined in a direction opposite to that of the last. The archegonium would have the appearance of a column consisting of four rows of cells, but for the fact that in all the cells of one of the four rows, immediately after the division of the cell of the second order by a radial longitudinal septum, a partition-wall appears which divides the cell into an inner three-sided cell, surrounded by other cells, and an outer cell, of which one of the four walls is free (Pl. V, figs. 3, 4). The young archegonium thus presents the appearance of a cylinder of cellular tissue, rounded above, consisting of a central string of cells (as many as thirty in number), which is surrounded by a single layer of four cells. The central cellular string does not extend quite to the base of the young archegonium, which base consists of a short stalk, of the height of one or two cells, and composed of four cells lying in the same plane (Pl. V, figs. 5, 6, 6^b). The cells of the central string become filled, soon after their formation, with a granular mucilage, in which the nucleus lies imbedded in the form of a transparent vesicle (Pl. V, fig. 4). The undermost of those cells swells considerably; its nucleus also increases in size (Pl. V, fig. 5). The adjoining cells divide by longitudinal septa as soon as the longitudinal growth of the archegonium is finished (Pl. V, figs. 5, 6, 7). The same division proceeds

to some extent (to the height of five cells), towards the apex of the archegonium, the lower part of which thus becomes enlarged. In the mean time, the horizontal septa which divide the cells of the central string of the archegonium from one another become dissolved (Pl. V, fig. 5). A canal, filled with mucilage, and closed above, thus originates in the longitudinal axis of the archegonium. The cells which form the arch over its upper end suddenly part from one another, bending themselves somewhat backwards; an open passage, not obstructed by any cell-wall, now leads from the outside through the entire length of the archegonium down to the large cell in its swollen lower part (Pl. V, figs. 6, 7). In the mean time there is formed in the large cell a free spherical cell, enclosing a central nucleus, and which, when fully grown, almost fills the cavity of its mother-cell (Pl. V, figs. 6, 7).

During the development of the first archegonia a thin lamella of cellular tissue grows out of the upper surface of the flat stem, from the point of insertion of the archegonia backwards. It follows the longitudinal growth of the archegonia, inasmuch as the cells of its fore edge continually divide by transverse septa, and its side edges unite with the thin prolongation of the shoot which extends itself underneath (in front of) the archegonium (Pl. V, fig. 2). A pouch-shaped covering thus originates, which is open in the fore part, and encloses the archegonium. It entirely corresponds in its whole development with the perianth of the leafy Jungermanniæ, especially in the fact that it appears at a later period than the first rudiments of the archegonia. Pellia must not be classed with the Gyromitriæ.

The above condition is attained by all those archegonia whose longitudinal growth is terminated before the time when the rudiments of the fruit begin to appear in one of the archegonia enclosed in the same perianth with themselves. The time of the development of the archegonia is very uncertain: the earliest open at the beginning of May; the latest in the middle of July. Even then, those flowers which contain no rudiments of fruit exhibit abortive archegonia, in which the walls of the canal of the neck and the wall and contents of the large cell in the expanded

lower portion are of a deep-brown colour. Of these abortive archegonia some have only just burst at the apex, some are still closed, and others again are in the earliest stages of development.

I consider those archegonia whose apices have just opened, and the cell-walls of whose necks have not yet become brown, as in a state ready for impregnation; and I believe that, in order to effect such impregnation, it is requisite that some, perhaps one only, of the motile threads formed in the antheridia should reach the funnel-shaped opening of the archegonium. I have not, indeed, seen the spermatozoa of Pellia in that position, even if such be the case with other liverworts, about which I shall speak hereafter. I have frequently found, however, that in those flowers of Pellia to which I had applied a drop of water containing ripe, opened antheridia, several (from three to seven) archegonia have produced the rudiments of fruit (Pl. V, fig. 9ᵃ). The circumstance, that the ripening of the antheridia and the bursting of the archegonia begin and end precisely at the same time, affords as good ground for the above view as the more exact knowledge which we possess with regard to mosses — a view, moreover, which in all essential points has been entertained for an equal length of time with regard to both liverworts and mosses.

The outer cells of the expanded portion of the impregnated archegonium divide rapidly several times one after another, by radial septa, by longitudinal septa parallel to the free outer walls, and by transverse septa; this cell-multiplication is most vigorous at the base of the archegonium. All the newly formed cells become filled with chlorophyll. Thus, very soon after the beginning of the development of the rudiments of the fruit, the expanded portion of the surrounding archegonium assumes the form of a somewhat large, dark-green, cellular mass. The neck of the archegonium remains unaltered.

The fruit is developed from the free spherical cell which is enclosed in the central cell of the expanded portion of the archegonium. That cell first divides by a transverse septum into a lower and an upper cell, of which

the former is much the larger of the two, and the latter has the shape of a segment of a sphere. The latter divides by a longitudinal septum shewn in Pl. V, fig. 8, which represents the rudimentary fruit extracted entire. Each of the two cells which have a semicircular basal outline is divided after previous expansion in length, by a longitudinal septum at right angles to the previous one, and each of the four cells thus formed is divided anew by a transverse septum. The young rudimentary fruit now exhibits four apical cells (cells of the first order). Its growth is carried on by continually repeated division of these cells by means of horizontal septa.

In the first four interstitial cells thus formed, cell-multiplication commences in the direction of their breadth and thickness. Each of these cells (whose form is that of the quadrant of a cylinder) divides by a longitudinal septum parallel to the axis of the rudimentary fruit, cutting both the side walls at an angle of 45°; and each of the four new outer cells thereupon divides by a radial longitudinal septum. In the next higher double pair of cells, the cell-multiplication does not proceed any further. From thence (going upwards) the division is repeated in the eight outer cells by a longitudinal septum turned towards the free outer surface, and the following division takes place by a radial longitudinal septum. By this time the rudimentary fruit has the form of a short club (Pl. V, fig. 9). Its upper end, however, soon increases considerably in thickness by divisions which take place in the cells of the apical surface by means of septa inclined outwards from the longitudinal axis of the organ, which divisions alternate with the longitudinal and transverse divisions of these cells. The cells of the apex of the rudimentary fruit exhibit, in consequence, when cut longitudinally, a regular radiate arrangement, which arrangement changes, in the lower part of the fruit, into one consisting of parallel rows of cells (Pl. V, fig. 10).

About two months after impregnation, the apical cells of the young fruit cease to divide. An active cell-multiplication begins instead in almost all its already formed constituent parts. The cells of the upper clavate end, excepting the innermost

of them, divide by septa parallel to a tangent to the nearest portion of the outer arcuate surface, which latter septa alternate with others at right angles to them, and with radial septa. The cellular mass, which thus increases in size, is the future capsule. In the middle of the rudimentary fruit the cells which eventually form its stalk divide, frequently several times over, by means of horizontal septa exclusively. There is thus formed a cylindrical column of about sixty (12 measured diametrically) vertical rows of small tabular cells. The lower third part of the rudimentary fruit ultimately exhibits a rapid increase in the number of its cells, both in length and thickness—an increase which diminishes gradually downwards. This end of the rudimentary fruit assumes in consequence the form of a turnip; its thickness very soon considerably surpasses that of the cylindrical middle portion (Pl. V, fig. 11). At this period an active multiplication commences in the cells of the circumference of the short upper protuberance of the swollen base of the young fruit. These cells, which form a girdle of about four cells in height, divide first by horizontal septa (Pl. V, fig. 11), and afterwards by septa parallel to a tangent to the circumference. By this means there arises out of the upper portion of the turnip-shaped enlargement of the fruit-stalk a hollow cylinder, enclosing its columnar portion. This sheath increases in length by continually repeated division of the cells of the free upper edge by means of alternately inclined septa. Its cells of the second order are soon divided anew by membranes at right angles to the latter septa, the older lower cells being divided more frequently than the upper younger ones. The free upper edge of the hollow cylinder consists, in all its stages of development, of a single layer of cells; towards the base the number of the cells continually increases. In the course of further development, four (in exceptional cases three) triangular flaps, enclosing the fruit-stalk upwards for a considerable distance, are formed from the edge of the sheath, by means of a locally increased intensity in the cell-multiplication in a longitudinal direction. During the formation of the sheath, the end of the fruit-stalk beneath it continues to increase in thickness; this increase terminates, as does also the multi-

plication of the cells of the sheath in a longitudinal direction, when the sheath has attained a length equal to a fourth or a third part of the stalk of the young fruit which is still enclosed in its calyptra (Pl. V, fig. 13). At an early period, even before the expiration of the third month from the commencement of the rudiments of the fruit, a differentiation of the tissue appears in its upper swollen end, *i. e.* the future capsule. The cells of the outer surface divide by septa perpendicular to this surface, and then again by partitions also perpendicular to the arched outer surface, cutting the last-formed septa at an angle of 90°. The inner cells take no part in this division; they appear, therefore, eight times larger than the others; in longitudinal and also in transverse sections, the boundary of each pair of cells of the outermost layer coincides with that of one of the adjoining inner cells (Pl. V, fig. 11). At the same time the walls of the inner cells of the young capsule begin to thicken. The substance of the thickened walls swells up very rapidly and extensively in water; to such an extent that, in cutting through a young fruit placed in water upon the stage of the microscope, the cells of the interior of the capsule immediately protrude laterally beyond the wall of the capsule. The swollen gelatine is dispersed in the water; the primordial utricles of the cells become free, and assume a spherical shape (Pl. V, fig. 12). In order to get an insight into the structure of the interior of the young capsule, it is indispensable that it should be examined in rectified spirit of wine. With tincture of iodine the entire mass of its cell-walls becomes coloured a vinous red or violet. Even after the differentiation of the wall from the inner tissue of the young capsule, the cells of both increase considerably. The cells of the lower part of the wall divide by septa parallel to the outer surface; consequently, at the spot where the wall of the capsule adjoins the fruit-stalk, that wall consists of two layers of cells. On the other hand, the cells of the wall of the upper part and of the apex of the young capsule divide exclusively by septa perpendicular to the outer surface (compare fig. 11 of Pl. V with fig. 13). At the same time the cells of the interior, especially those at the boundary of the wall of the capsule,

increase in all three directions; most actively in the neighbourhood of the apex. By the coincidence of both methods of multiplication of its cells, the hemispherical form of the young capsule is changed, within a month, into a long oval form (Pl. V, fig. 13).

By the end of August the walls of the cells of the interior are entirely broken up and undistinguishable. The free primordial utricles begin now to clothe themselves with new and firmer cell-walls. They then exhibit a very different deportment. One portion of the cells becomes elongated and spindle-shaped—the future elaters. A whole string of cells lying in the longitudinal axis of the young fruit assumes this spindle form; around this string the rest of the cells destined to form elaters are arranged, radiating upwards (Pl. V, fig. 37). Another portion of the cells of the interior assumes a spherical form: these are the mother-cells of the spores. In their fluid contents, very numerous small chlorophyll-granules now make their appearance.

The mother-cells retain the spherical form only for a short time. By the first week of September their walls exhibit four protuberances, each of which, situated at a distance of 120° from the neighbouring one, constitutes an arched surface, the basal outline of which is an equilateral spherical triangle. These bulgings of the cell-wall become rapidly more and more arched; by the middle of September each mother-cell appears to be composed of four oval sacs open at one end, which unite at an angle of 120° with the open, more pointed ends, so as to form a quadrangular median space (Pl. V, figs. 14, 15). Each of these bulgings of the mother-cell contains a nucleus; the mode of its origin, as well as that of the primary central nucleus of the mother-cell, (which latter nucleus has now disappeared,) is difficult to make out, on account of the opaque cell-contents, which consist of a thick mass of chlorophyll-granules. It is even somewhat difficult to feel assured of what is an undoubted fact, viz., the presence of a secondary nucleus in each of the bulgings of the mother-cell.

At the boundaries of the four protuberances of the mother-cell, the inner wall of the latter becomes much more thick-

ened than in its other parts. Six bands are formed, which are attached to the inner wall, and protrude inwards. At their first appearance, in the middle of September, they are tolerably flat, but increase slowly in height until the beginning of December (Pl. V, fig. 17). The median space by which the four protuberances of the mother-cell are in continuous communication * is thereby narrowed; rather narrow circular cavities lead from it to the four protuberances. It is now filled exclusively with transparent fluid matter as clear as water; chlorophyll-granules and granules of mucilage are as yet found only in the protuberances. Suddenly each of the latter appears separated from the quadrangular median space of the mother-cell, by a wall convex towards the interior (Pl. V, fig. 17). This delicate membrane is probably not mounted upon the edge of the broad ledge which protrudes into the median space, but clings to its surface, and encloses the entire contents of the protuberance, which, consequently, now represents a very delicate-walled oval cell, *i. e.* the young spore. By the dissolution of that portion of the wall of the latter cell which belongs to the protuberance of the mother-cell, the space very soon becomes free; I have reason to suppose that this occurs within forty-eight hours after the spore has become individualised. The six thickened bands, on the other hand, which consist of glass-like cellulose, and which unite to form the skeleton of an uneven-surfaced quadrangular figure, last for several days; they are to be found in large numbers amongst the escaped spores, and are most elegant microscopical objects (Pl. V, fig. 20).

The spores of Pellia exhibit in the course of their development several peculiarities, which are of importance in the study of cell-formation. That the walls of the special mother-cells grow gradually inwards from the inner wall of the mother-cell is placed beyond a doubt, as well by the slow growth of the bands above mentioned, as also by the fact that, in Pellia, the walls in question are normally only

* This appears perfectly clearly when one of the protuberances of a mother-cell which has been lying in water bursts, and a portion of the contents escapes through the fissure (a very frequent occurrence). The fluid contents of the uninjured protuberances of the mother-cell then flow slowly, mixed with chlorophyll-granules, into the one which has been ruptured.

developed to the extent of two third parts, and never combine to form partition-walls. If there were any need of additional evidence in opposition to the theory again brought forward by Karsten, viz., that vesicles too small to be seen with the microscope gradually grow into daughter-cells and occupy the entire space of the mother-cell, it would be afforded by the existence for three months before, as well as during and after the individualization of the spore, of a secondary nucleus in each of the protuberances of the mother-cell, which protuberances for a long period freely communicate with one another. The circumstance that the four protuberances of the mother-cell of Pellia, which eventually become the spores, leave a space between them filled only with water, is a convincing proof of the independent nature of the halves of the primordial utricle.

The young spore divides by a transverse septum very shortly after it has become clothed with a proper membrane; usually whilst it remains attached to its three sister-spores by the remnants of the mother-cell (Pl. V, figs. 18, 19). Upon the commencement of this process the central nucleus of the spore, disappears; two new nuclei, of a flattened ellipsoidal form, appear (Pl. V, fig. 18). The numerous small chlorophyll-granules through which the nucleus is faintly seen, thereupon appear separated into two groups, each filling one half of the spore, so that in its equator there is formed a narrow zone of transparent mucilaginous fluid, free from granules and chlorophyll-bodies. This light space appears suddenly traversed by a very delicate but sharply defined line, which is the side view of a septum passing through the spore (Pl. V, fig. 21). The same process is shortly afterwards repeated in each of the two semi-ellipsoidal cells which are thus formed (Pl. V, figs. 19, 22, 24). At this time (the beginning of December) one of the four middle cells sometimes divides by a longitudinal septum also (Pl. V, fig. 23). Henceforth the number of the cells of the spore does not increase until its dispersion in the spring of the next following year. The spore, however, secretes over its whole extent a brownish, slightly transparent outer membrane, covered on its external surface with numerous very small asperities, which, when the spore is

ripe, renders the boundary lines of the four or five cells of which the spore is composed very indistinct.

Under cultivation, irregularities in the development of the spores of Pellia are rather frequent. The primary halves of young spores sometimes divide by longitudinal septa instead of by transverse ones (Pl. V, fig. 25). Not unfrequently all the mother-cells of a fruit become abortive shortly before the period of the independent existence of the spores, excepting a few of the mother-cells, which in such a case attain almost double the usual size.

The vegetative development of the rest of the species mentioned in the title of this chapter differs materially from that of Pellia. The growth of *Metzgeria furcata* in length and breadth is discussed by Nägeli, in his essay on the study of cell-multiplication, "Wachsthumsgeschichte der Laub. und Lebermoose" ('Zeitschrift f. Botanik,' Heft 2). My view of the process, as the following remarks will show, differs in some subordinate points from that of Nägeli.

The longitudinal growth of the strap-shaped stem, which is slightly rounded at the apex, results from the continually repeated formation of septa, spreading right and left, and perpendicular to the surface of the stem (Pl. V, figs. 26, 27, 28). The cells of the second order thus produced, whose basal outline is a rather long five-sided figure, divide first by a septum at right angles to the side walls and perpendicular to the surface of the stem. In the outermost one of the newly formed cells the same process is repeated again: a septum appears parallel to the one last formed, or else this cell, as well as its inner sister-cell, divides by a longitudinal septum parallel to its side walls. In the former case the shoot grows in breadth; in the latter in length. In both cases the division is repeated several times, always in the outermost cells, by septa at right angles to the side walls. The development of each shoot begins with the second form of cell-multiplication of the cells of the second order; as the longitudinal growth draws to a close, the shoot is prepared for furcate ramification (Pl. V, fig. 28), and thus the first form of cell-multiplication steps in. In each of the masses of cells which are formed by the division of a cell of the second order, septa

parallel to the surface of the stem are only found in the one innermost cell adjoining the longitudinal axis of the shoot. After the first division of this kind, the formation of a horizontal septum is repeated twice in each of the under cells. The middle line of the stem consequently consists of two parallel rows of four tabular cells one above another; the remaining part of the stem is a single superficies of cells. Both the inner pairs of cells of the mid-rib which protrudes from the lower side, divide by longitudinal septa at right angles to the surface of the stem; they are, therefore, about half the size of the adjoining cells of the upper and under sides (Pl. V, fig. 29). Sometimes the cells of the underside of the mid-rib follow in this division. The under side of the fore edge of the mid-rib sends out numerous bicellular hairs with a swollen terminal cell, and which, bending themselves upwards, enclose to a certain extent the growing end of the stem. The entire under surface of the stem sends out rootlets, which are especially numerous on the mid-rib and the side edges. The young cells exhibit a nucleus with transparent fluid contents, which is freely suspended in the slightly granular cell-sap. The nucleus lasts for a long time, and, by means of the chlorophyll adherent to its exterior, it is perceptible even in older cells, where its contents refract the transmitted light much in the same manner as the fluid contents of the cell. The chlorophyll-granules of Metzgeria are amongst the smallest in the vegetable kingdom.

Adventitious shoots are often developed from individual cells of the edge or of the under side of the mid-rib of plants growing in dry situations. The cell-multiplication in such shoots, which is very easy to observe, takes place in precisely the same manner as it does in growing primary shoots (Pl. V, fig. 26). Vigorous adventitious shoots, whilst still very young, form a mid-rib in the same manner as the growing primary shoot, which mid-rib, by the division of the cells lying between the first cell of the adventitious shoot and the mid-rib of the primary shoot, is not unfrequently prolonged backwards to the mid-rib of the primary shoot. Sometimes, in unhealthy specimens, the formation of cells of the third order is entirely suppressed;

the shoot then consists simply of a double row of cells (Pl. V, fig. 25).

A third mode of origin of lateral axes takes place at the approach of fructification. On the under side of the mid-rib, attached not exactly in the middle, but laterally either to the right or left, there is formed, at some little distance underneath the end of the stem, a cucullate leaf, in the axil of which a branch is developed, but only to such an extent as to form a flat cushion-shaped process. On its upper surface are produced either archegonia or antheridia. The antheridia, in structure and development, are exactly like those of most of the leafy Jungermanniæ, *e. g. Radula complanata*. The archegonia, which are short and thick, and only six cells in height, are situated, like the antheridia, usually from four to seven in number, in the axil of a leaf. Their regular mode of cell-development resembles that of Pellia; in Metzgeria, also, the large size of the cells of the archegonium facilitates observation (Pl. V, fig. 30). I have not had an opportunity of investigating the development of the fruit of Metzgeria. In spite of the countless multitudes of apparently healthy archegonia and antheridia produced by the thick patches of *Metzgeria furcata*, which in our hilly districts clothe the masses of rock in shady, moderately damp localities, the fruit is very rarely met with. Probably, the cause of this remarkable fact is to be found in the drought which prevails in the habitats of the plants at the period of the ripening of the antheridia, viz., the middle of June.

The species of Aneura (*A. pinguis* and *multifida*), notwithstanding the great difference of their habit from that of Metzgeria, exhibit the same kind of development at the ends of the stem (Pl. VI, figs. 2, 11). There is, however, one essential difference, viz., that the cells of the second order, even before their division by the septa *perpendicular* to the surface of the stem, divide by septa *parallel* to that surface. This division is repeated rapidly and frequently, after the manner of the growth (in thickness) of Pellia (Pl. VI, figs. 3, 12), so that the shoot increases very rapidly in thickness; longitudinal sections through its growing end have a parabolic form.

The ramification of the stem takes place in the same manner as in *Metzgeria furcata*. In Aneura, however, the growth of *one* of the young shoots in a forward direction exceeds that of the other, which latter, at a very early period, appears in consequence to be pushed on one side. This more vigorous development takes place alternately and regularly on each occasion of the division of the end of the stem, occurring at one division in the shoot produced on the *right* side of the apical cell, and at the next division in the shoot produced on the *left* side. In consequence of this, Aneura exhibits a median principal axis, and lateral axes with normally limited growth. In the side shoots of *Aneura multifida*, whose longitudinal growth is arrested, the parts adjoining the terminal bud on the right and on the left often outgrow the former, so that the fore edge of the branch appears deeply indented, resembling at first sight the Marchantieæ (Pl. VI, fig. 1).

The ramification of Aneura and Metzgeria is therefore truly furcate, like that of the stem of Selaginella; that of Pellia is not truly so, but resembles the ramification of Viscum, the cause of which lies in the fact that the development of each terminal shoot in Pellia is limited.

The archegonia of Aneura originate at the apex of very short side-shoots of the second or third order. In their origin and nature they resemble those of Metzgeria. Underneath their point of attachment there is produced, contemporaneously with the commencement of their formation, a circle of small leaves, from four to six cells in height, consisting at the base of from three to four cells, and at the apex of a single cell.

When the large cell in the interior of the flask-shaped portion of the archegonium of *Aneura multifida* * first begins to be transformed into the rudiments of the fruit, a series of very active divisions, which last for a long time, commences in the cells of the archegonium, excepting those of its neck. The lower part of the archegonium thus becomes a clavate, fleshy mass, which attains the size of a millet-seed, even when the rudimentary fruit consists of

* I have not had the opportunity of examining the formation of the fruit in *A. pinguis*.

only eleven cells. The cells of the branch bearing the archegonia, which adjoin the place of attachment of the impregnated archegonium, also take part in this division. In consequence of this, unimpregnated archegonia are often carried up on to the oval cellular mass (the calyptra) formed by the amalgamation of the flask-shaped portion of the impregnated archegonium with the adjoining parenchyma of the stem. By this means the growing calyptra, which increases vastly in size, is bent upwards, so that its longitudinal axis is at right angles to the surface of the stem (Pl. VI, fig. 8).

The multiplication is very active in the cells of the calyptra immediately under its apex, with the exception of the epidermal cells, which continue of rather a large size, (Pl. VI, fig. 8), and grow out into long cylindrical papillæ (Pl. VI, fig. 4), upon whose outer wall a network of projecting bands is formed. The neck of the impregnated archegonium is usually thrust off at an early period (Pl. VI, fig. 8).

The development of the fruit itself corresponds entirely in essentials with that of Pellia (Pl. VI, figs. 5—8), but it is altogether of a more slender construction. The fruit-stalk consists of only two concentrical layers of cells; the enlargement at its lower end is much less developed; the cells destined to form the elaters and the rows of spore-mother-cells are already differentiated (as in Frullania) at the time when the entire contents of the young capsule consist of a single horizontal layer of cells. Each individual elater, however, divides by a transverse septum; each pair reaches from the base of the capsule to its upper arched roof.

The antheridia of *Aneura pinguis* originate in precisely the same manner as those of Pellia. A hemispherical or shortly cylindrical cellular body, consisting of four short longitudinal rows of cells, is formed by the multiplication of one of the cells of the upper side of the stem (Pl. VI, figs. 14, 15); by the division of one of its middle cells into an inner and an outer one, the ground is laid for the differentiation of an outer layer, and an inner cellular mass destined to produce spermatozoa (Pl. VI, fig. 12). A wall

of cellular tissue is raised round the antheridium by the multiplication of one of its adjoining epidermal cells. *Aneura multifida* produces buds, often in very large numbers, near the ends of its shoots. Some of the cells of the upper surface, not unfrequently whole groups of twenty or more, protrude outwards in the form of an arch, become quite filled with chlorophyll-granules, and divide by a septum passing transversely through the cell perpendicular to the surface of the shoot; the same thing occurs, but less frequently, in the cells at the edge (Pl. VI, fig. 9). The bicellular bud becomes free by the swelling up of the middle layers of the wall of its mother-cell into a gelatinous substance which expands largely in water, in consequence of which the outer lamella of the wall bursts, and the buds escape. Their form is that of a somewhat elongated ellipsoid, strongly constricted at its equator; its outline brings to mind that of many of the Desmidieæ (Pl. VI, fig. 10). The development of the buds into a new plant begins with the repeated division of one of their cells by alternately inclined septa.

CHAPTER III.

LEAFY JUNGERMANNIÆ.

THE transition from the leafless to the leafy Jungermanniæ is a very gradual one; it passes through an unbroken series of gentle intermediate stages. One genus (Diplolæna) which apparently coincides with Aneura in all its vegetative phenomena, except that it has inferior leaves, is followed by the peculiarly formed genus Blasia, whose stem when young exhibits, in transverse section, the form of an ellipse, and when more advanced, is drawn out in breadth so as to become foliaceous—a genus whose superior and inferior leaves differ in shape, the former having entire, the latter denticulate, margins. Allied to these is the genus Fossombronia, which has a stem only slightly expanded, but nevertheless always much flattened on the upper side, and bearing only superior leaves: this genus differs very little in the relative size of its stem and leaves from many of the leafy Jungermanniæ taken in the most limited sense.

The most remarkable member of this series of transitional forms is, beyond all question, *Blasia pusilla*. In perfect shoots, that is to say, shoots bearing bud-receptacles, the stem is so much widened that its edges seem to amalgamate with the horizontally-arranged superior leaves; these leaves have been somewhat generally considered to be, and have been described as, "segments of the flat stem." On the shoots just mentioned it is only the inferior leaves which look really like leaves; they are denticulate scales on the right and left of the longitudinal rib which protrudes from the under side, and which throws out roots (Pl. VI, fig. 16). At the upper end of the stem is found

the terminal bud, which is surrounded by closely crowded superior and inferior leaves, and which is usually very difficult to make out, on account of the buds situated near it and upon it; this terminal bud is a mass of cellular tissue, which, in shoots capable of further development, has a much-flattened conical form, whilst in shoots whose longitudinal growth has terminated it is flat and emarginate at the apex; it bears on its under side amphigastria, and on the other side scale-like, inbricated superior leaves. Numerous hairs, similar to those on the very young parts of Pellia and Aneura, are scattered amongst the most newly formed leaves (Pl. VI, figs. 17, 18).

It is well known that numerous reproductive buds are formed on the under side of the stem of Blasia. Their mode of development is very like that of the similar organs in Anthoceros. The contents of one of the inner cells of the tissue of the stem (which cells are only separated from the under side by a single cellular layer) become transformed into a cell occupying the whole cavity of the mother-cell. This daughter-cell changes into a roundish body, composed of small cubical cells, which contain numerous very small chlorophyll-bodies of a dark bluish-green colour. The cellular layer of the under surface of the stem which covers the reproductive buds becomes swollen to a hemispherical shape by the increase in size of the latter.

I have not seen these reproductive buds develope into young plants. Corda figures their germination in Sturm's Deutschl. Flora, II abth., taf. 32. Bischoff treats this figure as a product of the author's imagination. I do not agree with Bischoff's opinion. It is true that the branched rootlets which Corda represents are not found in any liverwort. This portion of the figure is, at all events, erroneous. I consider it, however, beyond dispute that the organs in question are really reproductive buds, judging from the analogy which they bear to the undoubted buds of Anthoceros which originate in like manner. If old buds of Blasia are opened under water, their cells separate from one another in the surrounding fluid. The like phenomenon occurs in the undoubted buds of Anthoceros and Riccia, if the surrounding tissue continues to retain its vitality

for a very long time. It depends, certainly, only upon the decay and internal disintegration of the buds.

Blasia differs from all other leafy liverworts in the fact of its producing these reproductive organs, but still more in the fact that the well-known flask-shaped bud-cups are formed upon its upper side.

The cell-multiplication of the terminal bud of Blasia very much resembles that of Anthoceros, or of the young plants of Pellia. The apical cell continues to divide repeatedly by septa inclined alternately upwards and downwards (Pl. VI, figs. 19, 20). The cells of the second order divide by a septum coinciding with the longitudinal direction of the stem, and perpendicular to its surface. The frequent repetition of the formation of these parallel septa in the two halves of the stem causes the stem to increase rapidly in width (Pl. VI, figs. 17, 18). By the division of the cells of the second order (and their daughter-cells) by septa parallel to the surface of the stem, the stem increases in thickness (Pl. VI, figs. 19, 20). At the spot where a bud-receptacle is about to be formed, this latter cell-multiplication ceases at a very early period, even as early as in the cells of the second order, whilst it continues in the neighbouring cells. A circular depression is thus formed on the upper side of the stem, close to its growing end, and quite covered by the youngest superior leaves (Pl. VI, fig. 20). Individual cells of the base and sides of each depression send forth clavate papillæ, which are soon separated from the original cavity of the mother-cell by a transverse septum (Pl. VI, fig. 20). After the apical cell of these short, hair-like papillæ has divided two or three times by transverse septa, the hemispherical terminal cell divides by a longitudinal septum. In this way a process of cell-formation originates, which soon leads to the production of a globular (or polyhedral) cellular mass, viz., a reproductive bud, which is attached to the above-mentioned depression in the upper surface of the stem, by means of a hyaline stalk, consisting of one or two narrow cylindrical cells, with clear fluid watery contents. The arrangement of the cells of the reproductive buds corresponds with that of the terminal bud of the stem (Pl. VI, fig. 21).

Soon after the commencement of the development of the first reproductive buds, the margins of the depression in which they originate become elevated like walls—the elevation commencing with the hinder margin (Pl. VI, fig. 20). A cylindrical tube, open above, is formed over the depression in which the buds are generated (Pl. VI, fig. 21). The cells of the bud-receptacle itself, and those of the lower part of its growing margin, take part in the longitudinal elongation which now commences in the tissue of the stem. The cells of the upper part of the above tube extend themselves upwards only; those of its free margin continue to divide by transverse septa. By this means the lower part of the bud-receptacle becomes elongato-lageniform; the open tube appears inserted in its upper end.

Reproductive buds now make their appearance on the inner-side also of the upper arched surface of the bud-receptacle. The inner cavity of the receptacle is filled, like those of the Marchantieæ, with dense transparent slime, in which numerous short greenish threads, too narrow to admit of being measured, are imbedded (Pl. VI, fig. 22). (Are they the rudiments of fungi?) A very striking peculiarity is exhibited by the rudimentary reproductive buds in these cells, which are destined for a process of active multiplication. Their contents are as clear as water. No nucleus of any kind is to be seen. It is only on rare occasions that solid bodies are found in the cell-sap, in the form of from one to three sharply defined, angular, very small bodies with exceedingly active molecular motion (Pl. VI, fig. 22^b). Concentrated tincture of iodine precipitates a scarcely perceptible quantity of a yellowish-brown substance upon the inner wall of the cell, even when the tincture is considerably heated. When the bud (omitting the stalk) has become 4-5 cellular, a nucleus is for the first time perceptible in each of the cells, contemporaneously with the appearance of the first small chlorophyll bodies, which are of a beautiful emerald green. The number of these increases considerably towards the period of the perfecting of the bud. At this time numerous drops of a clear, yellow, fatty oil make their appearance in the cells of the buds. The chlorophyll changes colour. Ultimately the

stalk of the ripe bud detaches itself from the wall of the receptacle; the bud is ejected through the narrow tube of the lageniform receptacle, and becomes free. The escape of the buds is doubtless caused by the pressure which the numerous, rapidly-growing young buds, necessarily exert upon the mucilaginous contents of their receptacle, which contents are thereby in constant motion towards the opening in its neck.

It is stated in some books that the bud-receptacles of Blasia are closed when young, and open at the top at a later period (see Nees v. Esenbeck, Naturgesch. d. Europ. Lebermoose, B. 3, s. 395). An incorrect figure of Hedwig's has probably given rise to this erroneous notion (see 'Theoria generationis,' ed. 2, t. xxx, fig. 9).

The germination of the German liverworts, irrespective of the very special wonderful development of the spores of Blasia (see the beautiful observations of Gottsche, N. A. A. C. L., vol. xx, p. 1; and the supplementary ones of Grönland, 'Ann. Sc. Nat.' ser. iv, t. i, pl. 3); exhibits at least three essentially different methods of development.

Frullania dilatata has the largest spores. They are longish and tetrahedral, with rounded edges and angles; more rarely spherical. The inner membrane is as clear as glass, and not very delicate; the outer one is thin, membranous, and of a yellowish-brown colour, beset at regular distances with circular groups of brown protuberances (Pl. XI, fig. 27). The contents consist of a yellowish, viscous fluid, in which numerous granules are suspended. In the middle point of the spore a roundish ball of opaque matter (a nucleus surrounded by granules) is indistinctly seen. The germination of the spores commences as early as the fifth day after sowing. Numerous very small chlorophyll bodies are formed in the fluid contents. The primary central nucleus disappears, and in its place are found two new ellipsoidal nuclei. From eight to twelve days after sowing, these nuclei appear separated by a delicate line, which is the side-view of a septum, dividing the spore into two cells (Pl. XI, figs. 20, 29). One of these cells divides rapidly and continually by alternately inclined septa (Pl. XI, figs. 30—34); the daughter-cells thus formed divide by radial septa. The

cells of the third order divide by septa parallel to the longitudinal axis of the germinating spore, and cutting the side walls at an angle of 45°. In the outermost new cells of the fourth order, vertical and radial septa are formed, and then horizontal septa. In this way the spore, in the course of a month, is transformed into an oval cellular mass, whose longitudinal diameter is from three to five times the length of that of the ripe spore. The outer membrane of the spore, which expands considerably, surrounds the continually-increasing cellular body for some time, until eventually it bursts (Pl. XI, figs. 32, 33); the remnants of it often remain for a long time adherent to the base of the cellular body (Pl. XI, fig. 37).

One of the basal cells of the germ-plant now grows into a root with a thick wall and a narrow cavity, precisely similar to those which are developed by the perfect plant (Pl. XI, fig. 35). All the cells of the upper surface of the germ-plant, excepting those of the apex, protrude outwards in the form of arched papillæ. Ten days later the first leaves sprout forth close under the apex of the germ-plant, placed opposite one another on the stem at equal distances (Pl. XI, fig. 37). The arrangement of their cells shows that their growth results from the repeated division of a cell of the surface of the stem, by means of alternately inclined septa at right angles to the surface of the leaf. The second pair of leaves stands exactly over the first; the two other rows of leaves of the older plants first appear at a later period. The form of these earliest leaves (ovato-acuminate) is moreover very different from the two-lobed closely-folded later leaves. The terminal bud of the stem is situated between the leaves, in the form of a blunt, conical protuberance (Pl. XI, fig. 38). In this bud also the growth manifestly results from the division of an apical cell, by means of alternately inclined septa.

The small globular spores of *Jungermannia bicuspidata* have a brittle, finely granular, brownish outer membrane; they contain a mucilaginous opaque fluid (Pl. IX, fig. 1). The cushion-like masses of Palmelleæ which are usually found under the patches of this liverwort afford a peculiarly suitable substratum for the germination of the spores. As

early as the eighth day after the spores have been scattered over the moist, slimy mass, the expanding inner membrane ruptures the outer membrane, and protrudes in a vesicular form through the fissure (Pl. IX, fig. 2). It contains numerous very beautiful, small, emerald-green chlorophyll bodies. The protruding portion of the inner membrane is soon divided from the remainder of it by a transverse septum. By continual division of the fore-cell (that one, namely, which is furthest from the remnants of the exosporium) by means of transverse septa,—which septa are always preceded (as in higher plants) by the appearance of two new nuclei in the mother-cell (Pl. IX, figs. 3—7)—the germinating spore is converted, within a month after it has been sown, into a simple row of cells, seven or eight in number.

In the apical cell, and often also in the interstitial cells, with the exception of the one or two lowest, division by longitudinal septa now commences contemporaneously with an active longitudinal growth of the germ-plant, which latter growth results from the division of the apical cell by means of alternately inclined septa. In this way there originates a small band, formed of a single layer of cells, lying side by side in pairs (Pl. IX, fig. 8), near the lower end of which a slight thickening of the cellular tissue is often found, originating from the division by more than one longitudinal septum, of some of the interstitial cells of the cellular thread produced by the germinating spore. The ribbon-shape of the fore-end of the germ-plant is soon changed to that of a cylinder through the division by radial longitudinal septa of the cells of the second order, produced by the division of the terminal cell by inclined septa (Pl. IX, figs. 10^{b} $11^{a,b,c}$). From some of these cells short cellular branches sprout out always close under the septum dividing the particular cell from the next higher one. These branches are soon separated from the inner cavity of their mother-cell by a transverse septum. They are arranged in two vertical rows, the lower being placed (with respect to their attitude) irregularly upon the germ-plant, the upper ones being very regularly alternate (Pl. IX, fig. 9). The lower ones do not undergo any change, but in the third or fifth, reckoned from below, division occurs by a transverse

septum; in the higher ones this division is repeated in the terminal cell, so that they present the appearance of 3-cellular rows of cells. Those which originate at a later period exhibit longitudinal septa in their basal cells, and a furcate ramification at the apex; they resemble now, even in their outline, the leaves of the plant (Pl. IX, fig. 9). Higher up, in more advanced germ-plants, perfect leaves appear in the place of the above rows of cells. Individual points of the wall of many of the cells of the underside of the germ-plant often develope, even at an early period, into root-lets, and penetrate into the substratum (Pl. IX, fig. 10). In isolated cases the longitudinal growth of the first shoot of the germinating plant is suppressed; a new shoot then arises near to, and underneath, the apex, whose cells exhibit, at a little distance above the place of origin of the shoot, the same arrangement as that which is found at the apices of germ-plants in a more advanced state of development, and which are commencing to form leaves (Pl. IX, fig. 12, 12^b).*

Jungermannia divaricata, Engl. Bot., and *Alicularia scalaris* (Pl. VII, fig. 11), of both of which I have found spores just germinating and half developed germ-plants, appear to germinate in the same manner, in all respects, as *Jungermannia bicuspidata*. The same is the case, according to Grönland (l. c. Pl. I), in *Sarcoscyphus Funkii* and *Jungermannia crenulata*. The germination of *Lophocolea heterophylla* coincides generally with that of *J. divaricata*. Here, however, the delicate brownish outer spore-membrane is not ruptured by the expanding inner membrane, but is only gradually stretched, until finally it disappears in the further progress of the germination. The small globular spores scattered over decaying bark, swell to three times their original size within a few days. Numerous chlorophyll bodies are produced at the same time in their fluid contents; a nucleus becomes clearly visible in the centre of the cell, and may even be seen, although with difficulty, whilst the spore is still enclosed in the capsule. This nucleus vanishes, and

* Grönland has observed that the germ-plant whilst exhibiting only a single row of cells, not unfrequently ramifies; a fact which I have not observed. (See 'Ann. Sc. Nat.' iv ser. 1, p. 15.)

two new nuclei make their appearance. The germinating spore divides into two halves by a transverse septum originating between the two nuclei. The same process is repeated in one of the newly-produced cells; in this way a short, simple row of cells is formed (Pl. IX, figs. 17—25). The terminal cell of the row swells to the shape of a head, and divides by a longitudinal septum. From the continual division of the terminal cells a small band of cellular tissue is produced, similar to the second stage of development of the germ-plant of *J. bicuspidata* (Pl. IX, fig. 26), and which, as in that plant, produces lateral regularly-placed hairs, hair-like roots on the underside, and finally, after further development, perfect leaves at its apex (Pl. IX, fig. 26). At the time of the first appearance of the latter I always found the oldest hinder part of the plant entirely dead.

The spores of *Radula complanata* are tolerably large, globular, and clothed with a brownish-yellow exosporium. In the fluid contents, which enclose numerous very small chlorophyll bodies, a very well-defined large nucleus is suspended (Pl. XI, fig. 16). Twenty-four hours only after sowing the spores upon moist bark the greater number of them begin to germinate; some lie quiescent for weeks, and then germinate suddenly. Two nuclei, which are very prominent as light circular spaces in the opaque cell-sap, appear in the place of the primary central nucleus. Between them a septum is formed, dividing the spore into two halves (Pl. XI, fig. 17). The division is repeated in the newly-formed cells, but by septa at right angles to the first septum (Pl. XI, fig. 18); four cells having the form of quadrants of a sphere have now been formed in the spore. Each of these divides, in the first instance, by a septum either parallel to the first-formed septum or perpendicular to it (Pl. XI, figs. 19, 20); the four four-sided ones of the newly-formed cells divide by septa cutting the last-formed septa at an angle of 90° (Pl. XI, fig. $20^{b,c}$). The body which has been formed by the division of the spore-cell, and which now consists of twelve cells, four central and eight peripheral ones, has now a well-defined cake-like shape. Henceforth, the multiplica-

tion of the cells takes place exclusively in the direction of one surface, with the exception of a single division of all the cells which takes place by septa parallel to the surface, sometimes at this period (Pl. XI, fig. 21), and sometimes rather later. The underside of the flat expansion sends out rootlets with very narrow cavities, exactly similar to those produced from the lower leaf-lobes of fully developed plants. The cells of the margin, as well as those of the middle, multiply continually by division caused by septa perpendicular to the surfaces of the plate-shaped body (Pl. XI, figs. 23, 24). Ultimately, five months after sowing, a small protuberance of cellular tissue is seen at the margin of the flat germ-plant, which is soon recognised as the first commencement of the leafy stem by the fact of its producing rudimentary leaves under its apex (Pl. XI, figs. 25, 26). The arrangement of the cells of the terminal bud of the young stem shows clearly that its longitudinal growth is the result of the continual division of an apical cell by alternately-inclined septa (Pl. XI, fig. 26).

The normal mode of cell-multiplication in the growing end of the stem of developed plants of the leafy Jungermanniæ, is most difficult to ascertain. The terminal bud protrudes very slightly above the place of origin of the youngest leaf; the older leaves embrace the bud more closely than in any other plants I know. Numerous hairs which are developed upon and between the youngest leaves interfere with the observation; the contents of the youngest cells (viz. a thick mucilage in which numerous, often closely-packed chlorophyll bodies are imbedded) are almost opaque; all which matters present almost insuperable obstacles to the observer. With the exception of the instances brought forward in treating of the germination, there have been but few cases in which I have arrived at clear results, viz., in *Frullania dilatata* (Pl. XI, fig. 9, 10), *Lophocolea bidentata* (Pl. IX, fig. 13), *Trichocolea tomentella* (Pl. VIII, fig. 4), and *Jungermannia bicuspidata* (Pl. VIII, 12, [a, b]); the shoots here examined were the few-leaved shoots which break out between the leaves, and which originate from adventitious buds. They all agree in essentials with one another, as also with the modes of development of the rudi-

mentary stem observed in the germination of different species. *One* apical cell divides continually by septa alternately inclined in different directions. In *Jungermannia bicuspidata*, and *Frullania dilatata*, these septa are directed alternately right and left; the apical cell has the form of a segment of a sphere. The cells of the second order are divided by radial longitudinal septa. In each of the three-sided daughter-cells a septum is formed, cutting the side walls at an angle of 45°, and dividing the cell into an inner and an outer one. The latter is divided by a radial longitudinal septum into two halves; the growth of the circumference, even in leafy shoots, terminates at this point in *J. bicuspidata* and many nearly allied species, such as *J. connivens*, and *divaricata*. In these species both layers of cells, but more frequently only the outer one, continue to divide by horizontal septa; the four inner cells again divide by longitudinal septa, parallel to the axis; and afterwards at least two, often four of the newly-formed narrow cells of the interior of the stem, divide by radial septa. The axis of the stem consists, consequently, of somewhat elongated cells, which are much narrower than those of the single cortical cellular layer. Hence, also, there arises the indication of a vascular bundle, traversing the longitudinal axis of the stem. At a similar stage of the development of the stem in thickness—the lowest which occurs in the vegetable kingdom, from the leafy mosses upwards—the germ-plants of all observed species make a stand; ultimately and by degrees thicker shoots are formed, which produce the rudiments of fruit.

The great variety of forms in the leaves of Jungermannia is only partly accounted for by the rules of development of their cells. Many of the most striking varieties of form in perfect leaves are produced by an anomalous expansion of small groups of cells, and a multiplication, commencing at a late period, in individual cells of the margin of the leaf. The same difficulties which interfere with a clear ascertainment of the structure of the terminal bud, hinder to a still greater extent the observation of the first stages of development of the leaves. I have only been able in a few cases to observe directly that the leaf originates in the continual

division of a single cell of the upper surface of the stem, which protrudes in an arched form, at an early period, above the bounding surface of the stem. One of these cases is *Fossombronia pusilla*. Here the leaf, at its first appearance, is exactly like a short hair; the papillæform protruding cell of the upper surface of the stem is soon separated from the original cavity of the cell by a transverse septum, and afterwards divided by a septum parallel to the latter, into a lower cylindrical, and an upper clavate cell. The fluid contents of the latter are tolerably transparent, those of the former exhibit numerous chlorophyll-granules (Pl. IV, fig. 25). The lower cell only, divides in rapid succession; first by a transverse septum, and then the lower one or both of the newly-formed cells, by a septum at right angles to the last, and to the surface of the young leaf (Pl. VI, fig. 27). The upper pair of cells of the third order divide by transverse septa; longitudinal septa appear in the lower one, followed by transverse septa again in the outer cells (Pl. VI, fig. 26). The like succession of divisions takes place in the lower of the two pairs of cells, which originated in the transverse division of the two cells of the third order adjoining the apical cell, and is repeated, (with the recurrence of the transverse division of the upper of these pairs of cells,) continually in the two newly-formed cells lying nearer to the base of the leaf on the right and left of the median line. In the mean time, by frequent longitudinal division of the marginal cells of the lower part, the leaf increases considerably in breadth (Pl. VI, fig. 28); the one longitudinal half is always more vigorous than the other. This multiplication lasts much longer at the base of the leaf, where it keeps pace with and ultimately exceeds the growth of the stem, than it does at the upper margin, towards which it gradually diminishes. Individual cells of the margin continue to multiply for a longer period than their neighbours, repeating in miniature, in the mode of their multiplication, the formation of the leaf; in consequence of this the leaf assumes its multi-angular shape.

The rudimentary appendages of the leaves of the Lophocoleæ are, as has been already observed, short rows of cells; the first rudiments of the leaves themselves are nothing

more than simple cells, produced by the cutting off of short papillæ by a transverse septum. This renders it in the highest degree probable that a single cell of the bounding surface of the stem is the mother-cell of the leaf. However at the period when the young leaf first appears above the surface of the stem, it consists, when viewed from above, of four cells arranged side by side, embracing more than a fourth part of the stem (Pl. IX, fig. 14). The two middle ones are considerably larger than the side ones. The foundation for the two-pointed form of the leaf is laid immediately upon the division of the middle cells by septa, both at right angles to the median line of the leaf, and diverging from it to the right and left. Each of the two middle cells of the 4-cellular fore-edge of the leaf developes a papillæform prolongation, directed forwards and at the same time obliquely outwards; the outline of each is parabolical, and each of them divides repeatedly by transverse septa (Pl. IX, fig. 15). The wide and low interstitial cells thus produced are divided from once to as many as eight times by septa parallel to the longitudinal axes of the teeth of the leaves. The activity of this cell-multiplication diminishes from below upwards; the tips of the teeth of full-grown leaves consist of short simple rows of cells. During the formation of the teeth, the number of the cells of the lower part of the leaf continues to increase considerably by longitudinal and transverse divisions. The septa there formed are not always at right angles, or parallel to the longitudinal axis of the leaf, but are often laterally inclined to a considerable extent (Pl. IX, fig. 16). Frequent irregularities in the arrangement of the cells are produced thereby, especially in *Lophocolea heterophylla*.

In the latter plant the growth of the teeth on those leaves which are intermediate between the two-pointed lower leaves, and the entire upper leaves, is caused by division of the terminal cells by alternately-inclined septa, not by septa parallel to one another.

Jungermannia bicuspidata, and the closely allied *J. connivens* and *J. divaricata*, comport themselves, in the matter of leaf-development, similarly to the Lophocoleæ. In these latter, however, the regularity of the arrangement of the cells is much greater; the cell-multiplication in the lower

undivided half of the leaf is very limited, often almost suppressed in *J. divaricata*. The first rudiments of the two points of the leaf in *J. bicuspidata* are of a very plump form (Pl. VIII, figs. 8—10). In *Ptilidium ciliare* an active multiplication of the cells of the superior leaves commences at a late period, and is more clearly defined than even in Lophocolea and *J. bicuspidata*. With it the formation of the leaf commences by the protrusion outwards in the form of an arch, of one of the stem-cells of the second order, close underneath its apex; the protruding cell assumes the form of a swollen seam, embracing nearly half the circumference of the stem (Pl. VII, fig. 9, *a*). The cell divides by a longitudinal septum radial to the axis of the stem; both halves of the seam are separated from the original cavity of the cell by septa parallel to the outer surfaces of the stem. Each of the two cells of the young leaf thereupon developes itself independently in length. Each arches itself outwards to some extent, so that the fore-edge of the leaf exhibits two very blunt points; thereupon each of the cells divides by a transverse septum, which separates the protruding portion from the original cell-cavity (Pl. VIII, fig. 9, *b*, where only half of the leaf is shown). This division is repeated continually in each of the two apical cells. Each interstitial cell (cells of the second order) is bisected by a longitudinal septum. The cells of the third order divide by septa, either parallel to the latter septum or converging to it (Pl. VII, fig. 51, *c*); thereupon the cells of the edge of the leaf grow out into the long cilia which give the specific name to the plant, extending themselves in the form of papillæ, and then repeatedly dividing in their apical cell by transverse septa (Pl. VII, figs. 7, 8). Ultimately, longitudinal septa are formed in the lowest of the cells of the second order of these excrescences of the edge of the leaf. In highly developed leaves new cilia spring from the marginal cells of these pointed appendages of the edge of the leaf, originating in precisely the same manner as the parts upon which they are borne. The leaf now consists of two symmetrical halves, which have only a single row of cells for their common basis, and are connected together at the bottom only to the extent of a single cell (Pl. VII, fig. 8). It is this transverse row of cells which, by repeated

bisection, commencing at a late period, forms the cellular surface, often $\frac{1}{2}'''$ in length, which carries the two-pointed heads of the leaf.

In *Frullania dilatata*, which is furnished with such wide leaves, the leaf, at its first appearance above the surface of the stem (the periphery of which at this period exhibits only four cells) consists of a single wide-stretched cell (Pl. XI, fig. 9). It divides at first, once or twice, by a transverse septum; the newly-formed cells then divide by longitudinal septa (Pl. VIII, fig. 3). Each cell of the lower pair is now divided by a septum coinciding with the longitudinal axis of the leaf, and parallel to the first septum (Pl. XI, fig. 8 $^{a, b}$). The two apical cells of the rudiment of the leaf then divide by septa almost at right angles to its longitudinal axis, thus forming three-sided superior cells of the first degree of the second order, and four-sided inferior transversely extended cells of the second degree. The latter are divided immediately after their formation into inner and outer cells by means of a septum parallel to the longitudinal axis of the leaf (Pl. XI, fig. 8 ^{c}). The like processes are repeated several times in the two apical cells of the young leaf, so that the latter soon assumes the form of an oval cellular surface, consisting of two inner rows of cells bounded right and left by a row of marginal cells. The leaf soon begins to increase in breadth by repeated division of the marginal cells by means of septa parallel to the margin of the leaf. At the same time the mode of multiplication of the apical cells changes; the division by means of a septum almost at right angles to the longitudinal axis of the leaf, is followed by a division by means of a septum, mounted upon the latter septum, and only slightly diverging from the median line of the leaf. The now four-sided elongated apical cells continue to divide by alternate longitudinal and transverse septa (Pl. XI, fig. 14). In the later stages of development of the leaf, the cells produced by the division of the two apical cells, both the marginal cells and the double row of inner cells adjoining the median line of the leaf, are divided soon after their formation by septa at right angles to the longitudinal axis of the leaf (Pl. XI, fig. 13). This division is followed by a division by means of septa inter-

secting the last-formed septa, and parallel to those lateral cell-surfaces which are turned towards the median line of the leaf. In the cells of the interior of the leaf this latter division occurs once only; in those of the margin it is repeated sometimes as many as eight times in the outermost cells. The lower part of the leaf thus increases considerably in breadth, in proportion to the increase in circumference of the stem. As the longitudinal growth of the leaf draws to a close, the two apical cells do not keep pace with one another in their multiplication; one of them is usually a generation in advance of the other (Pl. XI, fig. 14).

By the time that the leaf is of the height of four cells, one of the marginal cells of its base begins to protrude laterally in the form of an arch. The protuberance is soon separated from the original cell-cavity by a transverse septum. By repeated transverse division of the apical cell the latter is transformed into a row of flattened cells, into a ribbon-shaped appendage of the young leaf, embracing the stem (Pl. XI, fig. 8 ^{c}); this is the first rudiment of the lower lobe (which presses against the upper one) of the superior leaves. It increases in breadth by the division of its cells by means of septa parallel to the longitudinal axis. This cell-division is repeated much oftener in the marginal cells of that side of the lower leaf-lobe which is turned away from the upper lobe, than in those of the opposite side. It frequently does not continue in the cells nearest to the apical cell. This latter cell grows regularly into a club-shaped hair (Pl. XI, fig. 2).

After the form of the leaf is thus prepared the cells of its base divide by frequently alternating longitudinal and transverse septa. The outline of the leaf is not thereby changed, but the number of its cells is very much increased, and the space over which the upper leave-lobe coheres to the lower is considerably extended.

The first stages of development of the inferior leaves of *Frullania dilatata* entirely resemble those of the bidentate superior leaves of *Lophocolea bidentata*, two teeth being formed on the fore-edge in the same manner as

in the latter plant. Soon, however, a new process of cell-formation appears at the side-edges of the leaf, underneath the place of origin of these teeth; commencing by a lateral expansion of one of the marginal cells, followed by a cutting off, by means of a transverse septum, of the protuberance thus formed, and by repeated transverse division of the newly-formed cells. By this means the hitherto double-pointed leaf becomes four-pointed.

The leaves of *Radula camplanata* are developed in all their parts in a manner precisely similar to that of the superior leaves of *Frullania dilatata* (Pl. XI, fig. 15). In this species, also, the apical cell of the lower lobe after its last division usually grows out into a clavate hair (Pl. XI, fig. 1). The multiplication of the cells of the base of the leaf lasts for a considerable time after the termination of the division of the apical cells.

The arrangement of the cells in the leaves of the round-leaved common Jungermanniæ (*J. curta, crenulata, Alicularia scalaris*) very much resembles the later condition of the upper lobe of the superior leaves of Frullania; it answers exactly to the arrangement of the cells in the direction of the surface, of young shoots of Pellia (Pl. VII, fig. 21).

The leaves of the Jungermanniæ usually exhibit a very decided inclination to development in breadth. I know of no species in which a single apical cell divides by means of septa spreading alternately right and left, and in which the division lasts until the termination of the growth of the leaf. The development of the leaves of all Jungermanniæ agrees in this, that the leaf originates in the extension outwards of one or more cells of the bounding surface of the stem close underneath its growing apex, and the subsequent separation by septa of the protuberances thus formed from the original cell-cavity. This first rudiment of the leaf grows at first exclusively by division of the cells of its apex and edge. After a series of such divisions, sometimes after very few (in extreme cases, as in Fossombronia, and in Haplomitrium according to Gottsche, after one single division) there en-

sues a most active and long-continuing multiplication of the cells of the base of the leaf, which gives the leaf its final shape.

The leaf-development of the different Jungermanniæ, which I have endeavoured to describe in the preceding pages, may be looked at from one and the same point of view. However different at first sight the individual processes may appear, they may be looked upon collectively as a tendency in the longitudinal halves of the young leaf-rudiments to develope themselves independently, and often unequally. The upper and lower lobe of the leaves of Scapania, Frullania, Radula, &c., answer to the two tips of the leaves of Lophocoleæ, *Jung. bicuspidata*, Ptilidium, and others.

The mode of ramification of the Jungermanniæ is very difficult to unravel, on account of the nature of the terminal buds. I have not arrived at an entirely clear idea of it in any species. Many observations point to the conclusion that the normal ramification of the axis results from a genuine furcate division of the naked apex of the terminal bud above the place of origin of the youngest leaf (*e.g.*, Pl. VII, fig. 1, *Ptilidium ciliare*), and there is nothing opposed to this view. The cases which appear to contradict it (such as the development of new shoots out of the axils of the leaves of fruit-bearing, or even older branches of terrestrial Jungermanniæ), may be looked upon as the development of adventitious buds.

These shoots in *J. bicuspidata* often attain the length of several millimetres without producing leaves. They are, therefore, just the objects in which the nature and method of cell-multiplication in the apex of the stem of Jungermanniæ may be most conveniently investigated (Pl. VIII, fig. 12 ^{a,b}). The half-subterraneous shoots of *Haplomitrium Hookeri* often remain in like manner leafless for a considerable extent. These are the processes which Gottsche is inclined to consider as being true roots of this liverwort, which is entirely unprovided with rootlets ('Nova Acta Acad. C. Leop.,' vol. xx, 1, 275). I had the opportunity of convincing myself that the structure of the growing end of these shoots entirely coincides with that of the end of the stem (Pl. VII,

fig. 1). They grow by continually repeated division of a single apical cell by means of septa alternately inclined in different directions. These shoots are also remarkable from the fact that in the older portion of them each epidermal cell grows out into a short papilla (Pl. VII, fig. 2), an enlargement of the upper surface, which may serve as a compensation for the absent rootlets.

The antheridia of the liverworts are mostly axile, sometimes solitary (Jungermannia, Lophocolea, Radula, Madotheca), sometimes gregarious (Alicularia, Frullania), in the axil of the same leaf. They are only occasionally free, *i. e.*, not protected by covering leaves on the upper surface of the stem (Fossombronia, Haplomitrium). The formation of the antheridium commences by the protrusion outwards in the form of an arch, and to a considerable extent, of one of the cells of the upper surface of the stem, before the latter has ceased to grow in thickness, and by the separation, by means of a transverse septum, of the protuberance thus formed from the original cell cavity. In the cell thus formed, which protrudes above the surface of the stem, there sometimes commences a series of repeated divisions of the apical cell by septa alternately inclined in two directions (*Madotheca platyphylla, Fossombronia pusilla*). This series of divisions, however, is not of frequent occurrence. More frequently the primary cell of the antheridium is divided several times successively by septa parallel to one another. By this means it is transformed into a row of cylindrical cells, which is sometimes of considerable length, as in *Lophocolea heterophylla.* The terminal cell of this cellular thread swells in a clavate manner (Pl. XI, fig. 39). It divides by a septum diverging from its longitudinal axis; the upper one of the newly formed cells then divides by a septum inclined in the opposite direction. The cells of the second degree are divided by radial longitudinal septa; one of the cells of that upper pair of cells of the third degree which is nearer the apex of the antheridium, divides by a septum parallel to the longitudinal axis, and cutting the side walls of the mother-cell at an angle of 45°. The young antheridium now consists of a spherical group of cells—a central cell surrounded by

five cells—which is borne by an elongated cylindrical stem consisting of a single row of cells (Pl. XI, fig. 1, 40).

The cells of the latter continue to divide frequently by septa parallel to those already present. The central cell of the spherical head which it supports multiplies actively in all three directions by repeated bisections (Pl. IX, fig. 31; Pl. XI, figs. 2, 41), whilst the cells of its outer layer divide only by septa at right angles to the outer surface, and much less frequently than the central cell. The antheridium is now a spherical mass of small cells filled with mucilage, surrounded by a single layer of tabular cells containing chlorophyll (Pl. XI, fig. 3). In each of those smaller cells a spermatozoon is formed inside an ellipsoidal or spherical vesicle (Pl. VII, fig. 6; Pl. XI, fig. 42). When the antheridium is ripe, the cells of its outer layer* separate from one another (Pl. VI, fig. 37; Pl. XI, fig. 42); the vesicles containing the spermatozoa, which have become free by the dissolution of the walls of the cellules containing them, escape in the form of a mucilaginous mass. They disperse themselves under water, and commence a rotating motion. The wall of the vesicle bursts, the enclosed spermatozoon escapes either wholly or partially (Pl. XI, fig. 42), and moves about in the water, keeping up a perpetual rotation round the axis of the spiral which it presents (Pl. VII, fig. 12; Pl. VIII, fig. 3).

In the antheridia of those species in which division by alternately inclined septa commences even in the earliest primary cell of the antheridium, the essential parts, *i. e.*, the mother-cells of the first degree of the spermatozoa and their covering layer, are developed in a precisely similar manner. A long series of cells of the second degree fail to multiply, so that a cylindrical double row of cells (long in Madotheca, short in Fossombronia) represents the second stage of development of the antheridium. The free end of this cylinder swells up to a clavate shape; and in the two youngest cells the divisions now ensue which lead to the formation of the central cell and its covering layer.

* In some species (*e. g., Fosssombronia pusilla*) the granules of chlorophyll in these cells have by this time become yellow, as is the case in Anthoceros, and in the mosses.

Madotheca platyphylla exhibits a remarkable peculiarity. The cells of the covering layer not only divide very frequently by septa perpendicular to the outer surface, so that they appear proportionally small and very numerous in the perfect antheridium; but the lateral cells and those underneath the central cell divide also by septa parallel to the outer surface of the young antheridium; the upper ones once, the lower ones several times over. By this means the antheridium acquires a considerable size; the oval group of cells in which the spermatozoa are produced occupies only a small portion of its upper half. The covering of this group of cells consists also always of a single layer of cells (Pl. VII, fig. 5). The walls of the cells of the covering-layer are coloured a bluish-red by iodine.

The spermatozoa in the leafy Jungermanniæ are considerably smaller than those of Pellia. *Fossombronia pusilla* has the largest of all those which I have examined; the diameter of the vesicles in which they originate is $\frac{1}{510}'''$; those of the diminutive *Jungermannia divaricata* are a little smaller (Pl. VII, fig. 21); those of *Frullania dilatata* and *Madotheca platyphylla* are very small (Pl. VII, fig. 6; Pl. XI, fig. 42).

The development of the archegonia of the leafy liverworts corresponds exactly with that of the like organs in Pellia, the Marchantiæ, and the mosses. In Fossombronia and Haplomitrium these organs are produced in the axils of leaves; in the other genera treated of in this chapter they are found only on short lateral branchlets. In growing archegonia, however, the peculiar condition which occurs in Pellia and the mosses is seldom seen. In Pellia and the mosses it often happens that the formation of the cells of the axile string does not extend as far as the cells immediately adjoining the apical cell, a fact which is doubtless to be attributed to the slow, and consequently relatively limited development of the neck of the organ. The archegonia of the true Jungermanniæ, and of *Radula complanata*, are proportionately short and uniformly thick (Pl. VII, figs. 14, 15; Pl. VIII, figs. 1, 2; Pl. X, fig. 1; Pl. XI, fig. 1); those of Fossombronia (Pl. VI, figs. 29—33)

and of Frullania are remarkably distended at the place where the large cell at the base of the neck is enclosed; those of Frullania have a longer neck than any moss or liverwort, without exception, with which I am acquainted (Pl. XII, figs. 1, 3).

With a few exceptions peculiar to the Jungermanniæ proper (Pl. VII, fig. 15; Pl. VIII, fig. 2; Pl. X, fig. 1), the archegonia of the leafy liverworts agree in the fact that until the formation of the rudiments of the fruit, the mother-cell of the large cell at the apex of the distended portion, is enclosed only by a single layer of cells; and they also agree in the fact that the distended portion is only of moderate height, and that before impregnation only two or three, or at the most four cells, are to be counted between the lower arched surface of the above-mentioned large cell and the base of the archegonium.

The archegonia of the greater number of leafy liverworts are furnished with a peculiar cup or pitcher-shaped organ of later growth than the archegonium itself—the *calyx* or *perianthium* of authors. In all cases which have been observed, the first appearance of this organ is in the form of a closed ring, consisting of a single layer of cells.

This is the case in the very different perianths of Frullania and Radula, and of *Jungermannia bicuspidata* and *divaricata*. The first rudiment of the perianth is formed by a contemporaneous protrusion, outwards and upwards, of a belt of cells belonging to the apex of the stem, surrounding the archegonia; and by the separation of the protruding portion of the cells, from the portion lying within the body of the stem, by means of a transverse septum. The like form of division is repeated several times in the coronet of apical cells of the young organ. In *Radula complanata* it lasts until the perianth has completed the full number of its cells in the direction of its length. Here and there cells belonging to the margin are also at the same time divided by vertical septa, and thus the number of cells of the circumference is increased above (Pl. XI, fig. 1). The form of the perfect perianth of Radula is consequently that of a horn continually widening upwards, and closely compressed laterally; doubt-

less the result of the resistance of the almost contiguous fore and hind lobes of the enveloping leaves, between which the organ must develope itself.

A very different state of things is presented in *Jungermannia bicuspidata* and *divaricata*, and in *Frullania dilatata*. In these plants, and in the latter of them at a very early period, the multiplication of the cells of the free upper edge of the perianth ceases altogether. On the other hand there ensues an active multiplication of the basal cells by rapid and often repeated divisions, in *Jungermannia divaricata* and *cuspidata* chiefly by horizontal septa, in Frullania almost as vigorously by vertical septa (Pl. VII, fig. 14; Pl. VIII, figs. 1, 2; Pl. XII, fig. 2). The cells of the free edge of the perianth of *Jungermannia bicuspidata* grow at an early period into long teeth, with transparent contents and thick cell-walls (Pl. VIII, figs. 1, 2). The form of the organ passes from that of an open basket into a cylindrical, and thence into a clavate shape; the converging teeth close the opening over the half-ripe fruit. In *Frullania dilatata* the perianth during development becomes more and more distended (Pl. XII, figs. 1, 2). The mouth, a narrow ring, is lifted up higher and higher, reaches the height of the apex of the archegonium shortly after the completion of impregnation (Pl. XII, fig. 3), and by the time of the termination of the longitudinal growth of the perianth, is carried about five times higher, by the continuous multiplication, and ultimately extensive expansion of the cells of the base. At the time of the ripening of the fruit the number of the cells of the free edge of the narrow mouth of the perianth is not greater by one than at the first appearance of the perianth out of the surface of the stem beneath the archegonia, when it amounts to from sixteen to twenty. In *Alicularia scalaris* the intercalary cell-multiplication extends from the basal cells of the perianth, up to the tissue of the end of the stem which bears the archegonia. At the time when the rudiments of the perianth appear in the form of an annular border enclosing the young archegonia, the end of the stem is slightly convex.* During the growth of the perianth there ensues

* See Gottsche, l. c., p. 325.

an active multiplication in the direction of their growth (outwards and at the same time obliquely upwards) of the peripheral layers of cellular tissue of the apex of the stem. This multiplication extends downwards from the rudiments of the perianth to the second or third pair of leaves. By this process the end of the stem which bears the archegonia becomes depressed below the level of an annular wall-shaped enlargement of the cortex of the stem, which enlargement bears upon its upper margin the young perianth, and upon its outer surface the uppermost pair of stem-leaves. An expansion of the cells of the above enlargement, in a direction parallel to the longitudinal axis of the stem, ultimately raises the points of insertion of the upper leaves above the apex of the calyptra.

From an exaggeration of the same condition is produced the peculiar formation of the (abnormal) perianth of *Calypogeia Trichomanes*. Gottsche has shown* that the short few-leaved branch which springs laterally from the median line of an inferior leaf, bears upon its apex the archegonia which are immediately surrounded by the last leaves; the apex of this branch inclines upwards, and becomes a round fleshy knob.† Successful longitudinal sections perpendicular to the plane in which the surfaces of the leaves of the principal axis lie, and passing through this axis, and also through the young fruit-branch which lies laterally in the axil of one of its inferior leaves, proved to me that the latter branch, which at first is directed obliquely downwards, curves itself upwards, so that at the period of impregnation the archegonia are erect (Pl. X, fig. 1). The central cell before impregnation is exceedingly small. The completion of the impregnation is first recognisable by an unusually active multiplication of the cells of the central portion of the archegonium during its conversion into the calyptra; a multiplication which forthwith commences in the tissue of the fruit-branch immediately adjoining the base of the archegonium (Pl. X, fig. 1). The small-celled tissue thus formed, which bears the impregnated and the abortive archegonia, becomes developed into the fruit-sac. The

* 'Nova Acta Ac. C. L.,' xxi, p. 427.
† L. c., p. 488.

larger wide-celled moiety of the fruit-stalk above the former takes no part in this new formation. An active cell-multiplication continues to take place in the former tissue for a long time. In the cells undergoing division, transverse septa perpendicular to the convex outer surface of the fruit branch often make their appearance. The annular zone of new cells thus formed, which lies at the greatest distance from the archegonia, undergoes, immediately after its formation, a considerable longitudinal elongation, at right angles to the partition-walls by the formation of which the cells were individualised. This is the mode in which the end of the fruit-branch, which is originally cushion-shaped, becomes transformed into a pitcher-shaped organ (Pl. X, fig. 6).* The cells of the inner surface of its cavity are from four to eight times narrower than those adjoining them. This arises from a division of the cells of the inner surface, by means of longitudinal and transverse septa perpendicular to the free surface, which takes place after the last division of the cells adjoining them. These narrower cells expand into long papillæ directed rectangularly inwards, which almost entirely fill the cavity of the fruit-sac (Pl. X, figs. 6, 8).†

Shortly before the commencement of the dissolution of the transverse septa of the string of cells which occupies the longitudinal axis of the neck of the archegonium of *Fossombronia pusilla*, a small free cell becomes visible in the middle cell of the ventral portion of the archegonium, occupying about an eighth part of the cavity of the latter cell, and near its very distinct primary central nucleus. The contents of this small free cell are transparent, and it has a finely granular nucleus with no nucleolus. There can be no doubt that this cell originates in free-cell formation round a secondary nucleus. In archegonia a little more developed, this cell, which has considerably increased in size, quite fills the lower third-part of its mother-cell. The

* It is essentially the same process which makes the cavity of the ovary of epigynous Phanerogamia inferior, and by which the nucleus of many anatropal ovules which have massive outer integuments, becomes sunk within the integuments, except that in these cases, and especially in the latter, cell-formation and cell-expansion are not so clearly distinguishable from one another as in Calypogeia.

† Gottsche has given an elegant figure of a longitudinal section of a later condition of the fruit-sac, l. c., T. xxxi, f. 15.

primary nucleus of this latter cell has become indistinct, in fact hardly discernible; it is manifestly undergoing dissolution (Pl. VI, fig. 32). As soon as the canal which transverses the neck of the archegonium is completely formed by the dissolution of the transverse septa of the axile row of cells, no trace of the primary nucleus of the central cell is any longer perceptible. The free daughter-cell, the germinal vesicle, now occupies about two third parts of the central cell (Pl. VI, fig. 33).*

In those forms where the central cell of the archegonium is smaller, the germinal vesicle at the time of the opening of the apex of the archegonium, almost entirely fills the mother-cell (Pl. VII, figs. 15, 16; Pl. VIII, fig. 2; Pl. XII, fig. 1).

Most archegonia are not developed beyond this stage. The cell-walls, which adjoin the longitudinal canal of the neck, assume a chestnut-brown colour, as also the inner wall of the large central cell of the ventral portion. The spherical cell, which has originated in the latter, becomes transformed into a dark brown mass. In individual archegonia, however, seldom in more than one in the same inflorescence, a fruit is produced by continuous division of the spherical cell which has been formed within the central cell of the ventral portion. It is more than probable that the action upon the archegonium of the spermatozoa, emitted from the antheridia of the same species, is necessary in order to bring about the development of the rudiments of fruit. Where antheridium-bearing plants are found in the neighbourhood of those bearing archegonia, much fruit is met with; when the contrary is the case there is no fruit. The common *Lophocolea bidentata* is a remarkable instance; this plant usually has abundance of archegonia, but very seldom bears antheridia, and the fruit is proportionately rare.

Those species fructify the most abundantly which bear

* The nucleus of the germinal vesicle very much resembles the defunct primary nucleus of the central cell. This circumstance, and the rapidity with which the above-mentioned process of development is gone through, led me on a former occasion ('Vergleichende Untersuchungen,' pp. 37, 47, 67,) to look upon the nucleus of the germinal vesicle as identical with that of the central cell, and to assume that the formation of the germinal vesicle took place by means of free cell-formation round the primary nucleus of the central cell.

antheridia in the axils of the leaves of the shoot which has archegonia at its apex. This is the case with *Lophocolea heterophylla* and *Radula complanata*, and frequently, but not always, with *Jungermannia divaricata*, all of which are nearly allied to *Lophocolea bidentata*. *Frullania dilatata*, a very free-fruiting species, certainly does not very often produce antheridia. Here, however, the mode of growth of the plant, is such as greatly to facilitate the passage of the contents of the antheridia to the archegonia. The patches of Frullania, which are in a dry situation, and at some height from the bottom of the tree on which they grow, are those which especially produce antheridia. Whenever rain falls, or there is a heavy dew, a considerable quantity of water trickles down from the patches which bear the antheridia, to those beneath them in which the archegonia occur. Moreover, the quantity of fruit in Frullania, however abundant it may be, is not at all proportionate to the enormous number of archegonial branches which the plant produces. The greater number of the flowers (which only contain two or three archegonia) are abortive, and produce no fruit.

The structure of the perianth of the Jungermanniæ is no obstacle to the impregnation. In Radula, in Frullania, even in the Lejeuniæ, the development of the rudiments of the fruit commences before the margin of the perianth is raised above the apex of the archegonia. In *Jungermannia bicuspidata* also the development of the fruit often begins very early, when the perianth has still the form of a wide open basket (Pl. VIII, fig. 3), but often also (as is the case too with *J. divaricata*) at a considerably later period, when the perianth has assumed the form of a hollow cylinder, when its margin begins to become folded and to bend inwards. These instances, however, are just those which afford undoubted proof that even under unfavorable circumstances the spermatozoa can reach the antheridia. In perianths of both species which I have cut open longitudinally and placed quickly in water, I have several times most clearly seen spermatozoa in rapid motion, whirling actively around the archegonia (Pl. VIII, fig. 12). In the Jungermanniæ there is found at the aperture of all archegonia which have

recently opened, small globular drops, often in large quantities, consisting of a hyaline transparent slimy substance. They appear to be formed from the escaped contents of the canal which traverses the neck of the archegonium. In recently-opened archegonia of *J. bicuspidata* and *J. divaricata*, as well as of *J. bicrenata* and *Alicularia scalaris* (which archegonia by the commencement of the swelling of their ventral portion exhibited the first indication of the fruit-formation), I saw between these drops, delicate, more or less twisted, colourless filaments, in appearance and size exactly similar to the spermatozoa of those species, but motionless (Pl. VII, figs. 12, 17; Pl. VIII, fig. 3).

The first division of the mother-cell of the rudiment of a fruit takes place by a transverse septum, at right angles to the longitudinal axis of the archegonium, and to that of the future fruit (Pl. VII, figs. 12, 17; Pl. VIII, fig. 3; Pl. X, fig. 1; Pl. XII, fig. 3). In *Frullania dilatata* and *Calypogeia Trichomanes* the youngest, bicellular condition of the fruit is shortly oval; in *Jung. divaricata* it is somewhat more elongated, and in *J. bicuspidata* it is drawn out to a great length. The lower of the newly-formed cells continues (with rare exceptions) during the whole life of the fruit without division; the upper one divides either immediately by a longitudinal septum (as is almost always the case in *Frullania dilatata, Lophocolea heterophylla, Radula complanata,* and *Alicularia scalaris*), or else it divides once or several times by horizontal transverse septa (as in *J. bicuspidata,* Pl. VIII, figs. 4, 5, *J. divaricata,* Pl. VII, fig. 8); the division by a longitudinal septum first occurs in the apical cell of the very young rudimentary fruit which consists of a single row of from three to five cells.

A horizontal transverse septum is now formed in both the newly formed apical cells; each divides into an upper cell, having the form of a quadrant of a sphere, and a lower cylindrical one. A longitudinal septum bisecting the cell and radial to the axis of the young fruit is then formed in each of the apical cells, so that the rudimentary fruit now exhibits four apical cells. In Frullania this division commences normally in the pair of cells nearest to the basal cell (Pl. XII, figs. 6, 7). In Calypogeia the same phenomenon is frequent (Pl. X,

figs. 2, 4) but not normal (Pl. X, fig. 3). Henceforth, the number of the cells of the rudimentary fruit, in the direction of the longitudinal axis, is increased; at first exclusively by repeated contemporaneous division of its four apical cells by means of horizontal transverse septa at right angles to the axis of the fruit.

This kind of cell-multiplication shows itself in the most simple form in the few-celled rudimentary fruit of *J. divaricata*. Its apical cells contain colourless mucilage, rendered turbid by numerous large and small granules; the interstitial cells are coloured deep grey-green by numerous small chlorophyll-granules (Pl. VII, figs. 13, 19). After the transverse division of the four apical cells has been repeated eight or ten times, the longitudinal growth of the fruit is completed (Pl. VII, fig. 20). The double pair of cells which now forms the apex of the clavate rudimentary fruit, then remains for the first time unaltered; the three next, on the other hand, divide into inner and outer ones by means of septa parallel to the longitudinal axis of the fruit, and cutting the side walls at an angle of 45° (Pl. VII, fig. 20). The outer cells become the wall of the capsule; further divisions take place in each of them by means of longitudinal and transverse septa perpendicular to the free outer surface. The wall of the capsule shortly before it bursts usually has twenty-four cells in its circumference, and eight cells in its height; the cells being of an oblong tabular shape. By a series of divisions, occurring principally in radial and tangential directions, the inner cells become transformed, partly into rows of mother-cells, and partly into elaters. The elaters in *J. divaricata*, as in all true Jungermanniæ and also in Radula, extend horizontally from the inner wall of the capsule to the longitudinal axis. In all these the inner tissue of the capsule, from which the spores and elaters are formed, consists, from the moment of the differentiation of the capsule-wall from its contents, of a short slightly distended columella, formed of a double pair of cells, with a quadrantal basal outline (Pl. XI, fig. 6). The first divisions of the latter cells take place by septa perpendicular to the longitudinal axis of the fruit alternating with others

radial to it. In the cells destined to form elaters no transverse septa are formed, whilst their sister-cells by repeated division parallel to the axis of the fruit form rows of cubical cells—the spore-mother-cells. These are, therefore, arranged in rows, which radiate horizontally from the longitudinal axis of the capsule, each three of which are succeeded by an elater, and of which four (sometimes by displacement, as many as eight), are contiguous to each elater (Pl. VIII, fig. 7; Pl. IX, fig. 23).

Contemporaneously with the commencement of the differentiation of the capsule-wall of *J. divaricata* from its contents, (which takes place by division into outer and inner ones of three double pairs of cells of the upper clavate portion of the rudimentary fruit,) septa parallel to the axis of the fruit are also formed in the first and second double pairs of cells above the base of the young fruit; the outer ones of the new cells thus formed divide by radial longitudinal septa. As they expand considerably in breadth, and protrude arcuately outwards, they form the knobby protuberance by which the fruit is attached to the tissue of the stem which bears it (Pl. VII, fig. 20). The basal-cell and the pair of cells above it remain unchanged. On the other hand, the cells of that portion of the rudimentary fruit which lies between the basal enlargement and the bottom of the capsule,—*i. e.*, the fruit-stalk,—divide all together by horizontal septa. They thus represent quadrants of cylinders of very small height; the transverse diameter is from six to eight times greater than the altitude. A sudden longitudinal prolongation of these cells, to an extent manifestly far exceeding fifty times the original longitudinal diameter of the cells, lifts the capsule up (when the fruit is ripe), through the fissure of the ruptured calyptra, high above the perianth. I have found no trace of a flow of sap into the cells of the fruit-stalk in this species, although it is certainly the one best suited for such an observation.

The development of the fruit of the greater number of the Jungermanniæ agrees very closely with that of *J. divaricata*, and differs only by the more frequent repetition of certain cell-divisions, and by more vigorous develop-

ment in length and thickness. In *J. bicuspidata* (Pl. VIII, figs. 5, 7), and *J. tricophylla*, in *Radula complanata* (Pl. XI, figs. 4, 5), *Lophocolea heterophylla*, *Alicularia scalaris*, and *Calypogeia Trichomanes* (Pl. X, figs. 2-8), the four apical cells of the rudimentary fruit often divide repeatedly by horizontal transverse septa; the three-sided cells of the second degree thus formed divide, however, all together, by septa parallel to the tangent of the curved outer-wall, and cutting the side-walls at an angle of 45°. In *J. bicuspidata* (Pl. VIII, fig. 7), this division takes place once, in *Lophocolea heterophylla*, and *Radula complanata* twice (Pl. XI, figs. 4, 5); in the latter by a repetition of the division in the outer cells, after a previous formation of radial longitudinal septa therein. After the cesser of multiplication in the apical cells, the capsule-wall is produced by the continuous division of the outer layer (in Lophocolea, Radula, and Alicularia, of the *two* outer layers) of cells of the rudimentary fruit; by the multiplication of the elongated axile group of cells, formed out of four longitudinal rows of three-sided cells, are produced the elaters, which radiate from the longitudinal axis of the fruit to the capsule-wall, as well as the rows of spore-mother-cells, which are inserted between these in horizontal rows. The cells of the middle part of the rudimentary fruit assume a depressed tabular shape by repeated transverse divisions; collectively they form the fruit-stalk. In *Jungermannia bicuspidata* and *tricophylla*, the fruit-stalk normally consists of twelve longitudinal rows of cells, of four strings of three-sided cells traversing the interior of the stalk, and a layer of eight cells surrounding these standing at an equal elevation. In the cells of the outer layer transverse division ensues to a greater extent than in those of the central string; the latter are double the height of the former (Pl. VIII, fig. 7; Pl. IX, fig. 23). The fruit-stalk of Lophocolea, Radula, Alicularia, and Calypogeia (Pl. X, fig. 7), which, after the differentiation of the capsule-wall from its contents, consists of three concentrical layers of cells, continues to grow in thickness up to this period; in Radula the growth takes place by a single division; in Lophocolea and Alicularia by repeated divisions of the cells of its circumference.

By cell-multiplication extending on all sides, and diminishing downwards, the base of the rudimentary fruit becomes transformed into a turnip-shaped enlargement, sunk into the tissue of the fruit-bearing shoot. This enlargement is most vigorously and peculiarly developed (as is known from Gottsche's beautiful observations, 'N. A. A. C. L.' vol. xxi, p. 2) in the Geocalyceæ, where its upper margin grows into the sheath surrounding the fruit-stalk; and in Calypogeia, where it grows into a highly delicate membrane. A similar appearance is presented in *Alicularia scalaris*, which, in the formation of its perianth, in some respects resembles the Geocalyceæ: here four triangular fleshy lobes which surround the base of the fruit-stalk, are developed out of the enlargement of the lower end of the rudimentary fruit (Pl. VII, fig. 10). These are less conspicuous in the true Jungermanniæ, and in Lophocolea. *Frullania dilatata* exhibits hardly any indication of them (Pl. XII, fig. 9); lastly, in *Radula complanata* there is only a very moderate enlargement of the lower end of the fruit-stalk, produced by a transverse stretching and papillate expansion of the cells of its outer surface (Pl. XI, fig. 7).

The development of the fruit of *Frullania dilatata* (and doubtless also that of the nearly-allied Lejeuniæ) differs in its middle stages not immaterially from that of the proper Jungermanniæ. In Frullania the four apical cells of the rudimentary fruit divide, even at an early period, by means of longitudinal septa, which form an angle of 45° with the side-walls, but diverge at a sharp angle from the longitudinal axis of the fruit. The division of the apical cells afterwards proceeds in the same manner as in Pellia and Aneura. In the mean time the lower part of the rudimentary fruit increases considerably in thickness; the cells of its circumference divide repeatedly by longitudinal septa parallel to the axis, alternating with radial septa. The form of the rudimentary fruit is far less slender, its apex is proportionately far wider, than in *J. bicuspidata* or *Radula complanata* (Pl. XII, fig. 8). The elaters and the spore-mother-cells are produced by the multiplication of a horizontal stratum of cells, which is separated by a double layer above it from the cells of the apex of the rudimentary

fruit. This production takes place after the multiplication of the apical cells of the young fruit in a longitudinal direction has terminated (Pl. XII, fig. 8). The two covering layers of cells form the capsule-wall, having first multiplied considerably by often repeated longitudinal and transverse divisions which take place by septa perpendicular to the outer surface. The capsule-wall, in consequence of the rapid increase of the number of its cells, eventually becomes hemispherical (Pl. XII, fig. 9). Most of the somewhat elongated cells of the horizontal cellular surface, enclosed by the capsule-wall, follow the progress of the latter as its arched surface becomes elevated, dividing repeatedly by transverse septa; some, however, expand only in a longitudinal direction until they eventually assume the form of narrow cylindrical tubes, parallel to the longitudinal axis of the fruit. These tubes are attached at the base to the upper end of the fruit-stalk, and at their apices touch the inner arch of the capsule-wall (Pl. XII, fig. 9). The latter are the elaters; the tessellated cells produced by the division of the elongated cells, become the spore-mother-cells.

Contemporaneously with the earliest period of the development of the rudimentary fruit of liverworts, there commences a very active multiplication of the peripheral cells of the ventral portion of the archegonium, which thus becomes the calyptra. The cell-division, which occurs repeatedly and in rapid succession, often extends far downwards into the tissue of the branch which bears the impregnated archegonium. Whilst the lower part of the archegonium becomes transformed into the upper half of the calyptra, its distended form becomes compannulate (*J. bicuspidata*, Pl. VIII, fig. 6; *Radula complanata*, Pl. XI, fig. 4). The lower portion of the calyptra is formed out of the upward-growing tissue of the tip of the shoot upon the apex of which the archegonia stand. The abortive archegonia often appear pushed up high on the side-walls of the calyptra, which has originated from the impregnated archegonia (Pl. XI, fig. 4, *Radula complanata*).

No distinction can be traced between the base of the

calyptra in many liverworts (which is produced by the multiplication of the cells of the apex of the stem), and the vaginula of the mosses. In *Radula complanata*, for instance, the base of the calyptra is not less remarkably conical and fleshy than in Phascum. This multiplication of the cells underneath the impregnated archegonium in the direction of their thickness, is very active in *Radula complanata*, less so in Lophocolea and the true Jungermanniæ; lastly, in *Frullania dilatata* it is entirely wanting; here the multiplication of the cells is limited exclusively to the ventral portion of the impregnated archegonium, towards the base of which it diminishes considerably. The form of the calyptra in this species is flask-shaped in all stages of its growth; it is narrowly constricted at the base (Pl. XII, figs. 3, 5).

The lower, reduced end of the rudimentary fruit, extends downwards to the same distance as the cell-multiplication beneath the impregnated archegonium extends upwards into the tissue of the stem (Pl. VIII, fig. 6; Pl. XI, fig. 4). The arch of the basal cell of the end of the stem often exhibits a marked thickening of its wall (Pl. VIII, figs. 4, 5); perhaps it is by means of this that it acquires sufficient firmness to penetrate the cells of the yielding tissue which lies in its way. In *Frullania dilatata* the cavity of the calyptra, which encloses the young rudimentary fruit enlarges soon after impregnation by a multiplication of the cells of its walls, often so rapid and considerable, that the growth of the rudimentary fruit cannot keep pace with the increase in circumference and height of the cavity, which is filled with mucilage; at this period the young fruit often lies quite free in the interior (Pl. XII, fig. 4).

Gottsche observes a similar phenomenon in *Calypogeia Trichomanes*.* I have convinced myself by an observation made in 1853, that in Calypogeia, also, the development of the impregnated germinal vesicle normally follows step by step the great enlargement of the central cell of the archegonium, which is produced by the multiplication of its neighbouring cells. Both developments are slow, that of the

* L. c., T. xxx, f. 8, 11.

germinal vesicle into the fruit the slowest. After the completion of the rudiments of the fruit-sac, the calyptra has only increased moderately in size, and the impregnated germinal vesicle is still undivided, although doubled in length. In the fruit-sac, when from 1 to 3 mm. long, the rudimentary fruit is only 4-8 cellular (Pl. X, fig. 8). At all stages of development it entirely fills the cavity of the calyptra. The condition figured by Gottsche is certainly a diseased one; the rudimentary fruit, developing itself feebly, could not follow the growth of the walls of the archegonium.

In certain Muscineæ (*Pellia epiphylla*, *Jung. divaricata*, *Phascum cuspidatum*), and also in some vascular cryptogams (*Pteris aquilina*, *Aspidium Filix-mas*, and *Salvinia natans*), where several archegonia of one and the same group have been impregnated, the less developed of these archegonia have afforded me similar cases decisive of the point that the increase in size, and the form of the growing base of the archegonium, is not produced by the contact of the rudimentary fruit or of the embryo. In all these cases, moreover, two archegonia of the same prothallium had been impregnated; the arrest of development of the embryo had occurred in the less-perfect archegonium, which had manifestly been the latest impregnated and insufficiently nourished.

In the leafy as well as in the leafless Jungermanniæ the individualization of the elaters and spore-mother-cells is preceded by a considerable thickening of their walls, and the conversion of the substance of these walls into a material which swells up extensively in water. The mass of the thickened cell-walls often swells up in water more rapidly and to a greater extent than even in Pellia; in *J. bicuspidata*, *Radula complanata*, and *Frullania dilatata*, the determination of the arrangement of the cells of the interior of the young capsule is thereby rendered extremely difficult. In all the species which I have examined the substance of the walls, when moistened with tincture of iodine, became quite blue. In the mother-cells of the large-spored *Frullania dilatata* four protrusions of the wall (quite similar to those of Pellia, before mentioned,) and the gradual increase in size of the inner wall of the superimposed

ridges, which by their ultimate confluence become the septa of the special mother-cells, are clearly perceptible (Pl. XII, fig. 10). These special-mother-cells in *Frullania dilatata* exhibit delicate pits (Tüpfel) similar to those of *Anthoceros punctatus*.

The wall of the half-ripe capsule of most Jungermanniæ consists of a double layer of cells (*J. bicuspidata, trichophylla, Frullania dilatata, Radula complanata*). As the fruit approaches maturity the inner of these cellular layers is usually dissolved, and displaced by the growing spores.

The individualization of the cells of the interior of the capsule depends, as in all similar cases, upon a highly advanced state of this change in the properties of the substance of the wall of the outer layer of the affected cell-membrane. There exists, however, a striking difference between what occurs in Jungermanniæ, and the analogous processes in the development of the spores of other mosses and vascular cryptogams, and of the pollen-cells of Phanerogamia. In Jungermanniæ a thick layer, constituting almost the entire mass of the cell-membrane, undergoes transformation into a substance which becomes distended in water into a gelatinous mass, and disperses itself through the fluid; whilst in other cases this modification of the cell-membrane is limited to an immeasurably thin external layer. In many cases, even in Jungermanniæ, the condition of the different layers of the mother-cell-membrane during the distension varies. In *Fossombronia pusilla* the inner layer of the wall of those cells which are exclusively developed into elaters is so vastly distended by water when in a young state, that it bursts the outer layer of the cell-membrane (Pl. VI, fig. 36). The same state of circumstances, somewhat modified, occurs in the mother-cells of the same plant, where, however, the less-distendible outer layer is so thick that it does not burst; the expansion of the inner layer takes place at the expense of the volume of the cell-contents, which are compressed into a smaller space (Pl. VI, fig. 35). In *Blasia pusilla* also the membrane of the cell, from the division of which two spore-mother-cells have arisen, and which is very often present after the formation of the tertiary nucleus, resists the action

of water more than the membrane of the spore-mother-cells themselves (Pl. VI, fig. 23). The mother-cells of the spores of all the true Jungermanniæ which I have examined, those of Radula and Frullania, are rich in chlorophyll-granules. In *Blasia pusilla* the presence of chlorophyll is limited to the tertiary nuclei destined for spore-formation, the substance of which seems usually to be coloured green throughout (Pl. V, fig. 24).

The first investigations into the germination of the spores of Jungermanniæ, are those of Hedwig.* They extend no further than the protrusion of the first rootlet. The observations published by Nees von Esenbeck,† do not advance the knowledge of this subject to any further point. Bischoff, eighteen years later,‡ directed attention to the germination of Pellia, up to the formation of the first shoot.§ Bischoff's observations agree entirely with those of later observers, even in the unimportant circumstance that he represents the base of the germ-plant (the hinder part of the multicellular spore) as a globular enlargement of too great thickness. I have already spoken of the incorrectness of the expression (Vorkeim) applied by Gottsche to the first shoot of the germ-plant. Gottsche noticed,‖ although not very clearly, the multicellular nature of the spores of Pellia, and followed their germination, cell by cell, until the perfect development of the first shoot, stating more intelligibly the relation of the exosporium to the germ-plant. Gottsche at the same time published an account of the remarkable germination of *Blasia pusilla;* he showed that when the spore (after being sown) has become indistinctly multicellular, a long, cylindrical, tubular cell shoots forth, the end of which is developed into a cellular body, from which at a later period the stem of the germ-plant is produced. Lastly, Gottsche gave the first account of the germination

* 'Theoria generationis,' Leipz., 1798, 17.

† 'Nova Acta,' A. C. L. N. C., xiii, 1 (1824), 165.

‡ 'Handb. bot. Terminologie,' Bd. ii, Nurnb., 1842, 733, t. lvii, 2795-96. These observations appear to have been made as early as 1828. See 'Bot. Zeit.,' 1853, 14.

§ Bischoff completed this work at a subsequent period by the publication of further figures. See 'Bot. Zeit.,' 1853, t. ii, f. 14—21.

‖ 'Nova Acta,' A. C. L., vol. xx, pars 1, 382.

of the spores of a leafy Jungermannia, *J. crenulata*.* That account does not extend beyond the formation of a short filament from the inner spore-cell. After Gottsche's observations no notices of the germination of Jungermanniæ appeared until my own, mentioned above. At a later period Grönland† published his investigations of the germination of the leafy Jungermanniæ. He showed that the formation of the long, cylindrical tube discovered by Gottsche in the germination of Blasia was suppressed in cases where the spores were very thinly sown; that under these circumstances the spore immediately assumes the form of a cellular body, similar to that which, when the spores are sown thickly, originates in the end of each tube.‡ He pointed out, moreover, the occasional ramification of the prothallium of leafy Jungermanniæ,§ and extended the observation to some species hitherto not investigated or only imperfectly so—*Sarcoscyphus Funkii*, *J. crenulata*, and *Alicularia scalaris*, the development of which in other respects exhibits nothing peculiar.

The first important observations as to the mode of growth and cell-multiplication of the ends of the stems of Jungermanniæ are those of Nägeli.‖ He pointed out the mode in which the terminal cell of the leafy axis of *Metzgeria furcata* divides by alternating septa, directed obliquely right and left perpendicular to the surface of the stem, and the way in which the cells of the second degree thus formed produce, by continued bisection, the entire mass of cellular tissue of the flat stem. He showed further that the growth of the stem which¶ is developed from the gemmæ of *J. exsecta*, and that of the end of the stem of *J. trichophylla*,** was produced by continual division of a single apical cell, by means of oblique septa, of the same or a like inclination, but differing in position. I have not obtained from my own observations of the leafy Jungermanniæ any ground of

* *l. c.*, pp. 387, 391.
† 'Ann. d. Sc.,' iv sér., t. i, p. 1.
‡ *l. c.*, p. 20.
§ *l. c.*, p. 16.
‖ 'Zeitschrift f. wiss. Bot.' H. 2 Zurich, 1843, 138.
¶ *l. c.*, p. 166.
** *l. c.*, p. 172.

support for Nägeli's assumption that these septa are turned, not in two opposite directions only, but in several directions.

With respect to the ramification of the Jungermanniæ, the books afford but little information. I find no mention by any earlier observer of the difference, to which I have called attention, between the true dichotomy of Metzgeria and Aneura and the pseudo-dichotomy of Pellia. The remarks made by C. G. Nees v. Esenbeck, with respect to the ramification of the Jungermanniæ, have reference only to the fully developed condition.* His statement that the place of insertion of a branch in the principal axis is frequently not determined by the position of the angle of the leaf, in other words, that it is not found above the median line of the next lower leaf, afford as much support to my conjecture that the normal ramification of the leafy Jungermanniæ is a true dichotomy, as does the figure which Gottsche gives of a leafless subterraneous shoot of *Haplomitrium Hookeri* divided into two branches beneath the apex.†

With respect to the development of the *leaves* of Jungermanniæ, Gottsche's important statement must be remembered, that in *Haplomitrium Hookeri* the leaf, when quite young and consisting of only a few cells, bears at its apex (or when multi-angular at each of its angles) a clavate, bent, rètort-shaped cell, which, in a fully developed leaf consisting of a great number of cells, is still found in the corresponding position.‡ This observation, once made, afforded proof that the cell-multiplication in the leaf of Jungermannia is not the result of a continued multiplication of *one* apical cell.

The knowledge of the structure of the archegonia of the Jungermanniæ was, like that of the similar organs in the mosses, first established by Hedwig.§ He figures the archegonia as organs closed before impregnation, as open at the

* 'Naturgeschichte Europ. Lebermoose,' i (Breslau, 1833), 17.
† 'Nova Acta,' A. C. L., xx, pars i, t, xiii, f. 1.
‡ *l. c.*, pp. 275, 276.
§ 'Theoria generationis,' Leipz., 1798, 164.

top at the time of impregnation, and then traversed in the longitudinal axis by a canal; as organs out of which at a later period the calyptra, crowned with the neck of the archegonium, is developed. Our knowledge of the structure of these organs had made no progress since the time of Hedwig until my own observations were published.*

Prior to my own observations, the very young condition of the fruit had only been seen by Gottsche twice in *Calypogeia Trichomanes*, in the form of a two- or three-celled body at the base of a wide cavity of the calyptra, and which Gottsche considered to have sprung from the base of such cavity.† At a somewhat later stage of development of the young fruit, Gottsche saw indications of the formation of the same out of four rows of cells trending downward to the one basal cell, but he could not make out the matter clearly. Schmidel had already observed the well-defined limits between the lower end of the fruit-stalk and the tissue of the stem into which that end is sunk;‡ as also had Hedwig,§ who had observed the many toothed sheath around the base of the fruit-stalk in *Pellia epiphylla*.

With respect to the development of the spores of the Jungermanniæ, H. von Mohl established the fact that they are formed in fours, in round mother-cells, and that the elaters, as long as the spores are lying unformed in the mother-cell, have the shape of spindle-like, delicate-walled cells, standing in no organic connection with the spore-mother-cell. Von Mohl also observed that the young oval spores of *Pellia epiphylla*, whilst still hanging together in fours, are only in contact with one another by a small portion of their upper surface.‖

The membrane of the perfect elater had been noticed by Von Schmidel in *Aneura multifida*.¶ Nevertheless, the notion of "*naked elaters*" was prevalent until a recent

* Compare C. G. Nees v. Esenbeck, l. c., p. 60; Gottsche, l. c., p. 315.
† 'Nova Acta,' Ac. C. L., xxi, pars ii, 445, 447.
‡ 'Icones plantarum,' iii, Erlangen, 1797, Tf. 57, f. 14, *J. exsecta*.
§ 'Theoria generationis,' t. xvii, f. 10; *J. nemorosa*, t. xxiv, f. 4; xxv, f. 2, *Pellia epiphylla*.
‖ 'Flora,' 1833. 'Vermischte Schriften,' p. 68.
¶ 'Icon. plant.,' t. lv, f. 13.

period; Gottsche first put a final end to it* by showing the destructibility of this membrane by sulphuric acid, the action of which was resisted by the substance of the spiral thread. Gottsche showed also that the coloured thickenings of the cell-membranes of the capsule-walls comport themselves in this respect like the spiral thread of the elaters, and by this discovery was in a position to give the most satisfactory representations of the course of these thickenings of the walls of the elater-cells and of the cells of the capsule-wall.†

We are indebted to the same author for an explanation of the development of the perianth of the Jungermanniæ. He showed ‡ that the perianth in the Jungermanniæ is formed in the same way as in *Marchantia polymorpha*, where it had been observed by Hedwig § and Mirbel, ‖ and where it takes place at a late period, after the commencement of the formation of the fruit; he described the development of the perianth of the principal types, and showed that the involucre of Trichocolea is nothing more than the very fully developed calyptra, similar to that of Aneura.

Schmidel's discovery of the self-motile bodies in the antheridia of a cryptogamic plant was made in a Jungermannia, in *Fossombronia pusilla*.¶ The attachment of the antheridium to a stalk is first well figured by Hedwig in the same plant.** The first figure of the spermatozoa of a Jungermannia—*Aneura pinguis*—was given by Meyen.†† The existence and nature of these bodies had in the mean time been discovered in Sphagnum by Unger, and the cilia by Thuret in Chara. Gottsche afterwards figured those of *Haplomitrium Hookeri*, *Alicularia scalaris*, and *Fossombronia pusilla*;‡‡ lately Thuret has given those of *Pellia epiphylla* and *Fossombronia pusilla*.§§

* 'Nova Acta,' A. C. L., xx, pars i, 360.
† *l. c.*, t. xvii, f. *a—d*.
‡ *l. c.*, p. 544.
§ 'Theoria generationis,' p. 177, t. xxvi, f. 6, 7.
‖ 'Mém. Acad. des Sc. Inst. de France,' xiii (1835), 380.
¶ 'Icon. plant.,' p. 85.
** 'Theoria generationis,' t. xx, f. *a*, *a*.
†† 'Neues system der Pflanzenphysiologie,' Bd. iii (1839), t. xii, f. 39, 40.
‡‡ 'Nova Acta,' A. C. L., xx, pars i, t. xvi.
§§ 'Ann. d. Sc.,' iii sér., t. xvi, 10, 11.

Gottsche is of opinion that the antheridia of the liverworts in general have a wall consisting of a double layer of cells—an inner layer, the cells of which become detached when ripe and contain colouring matter, and an outer layer of hyaline, tubular cells, of small height, with transparent fluid contents. Gottsche's opinion is founded mainly upon investigations of *Haplomitrium Hookeri*. He attributes a similar structure to the antheridia of Fossombronia.* He is decidedly in error in both cases; the covering layer is certainly a single layer of cells, which, when the organ is fully ripe, give way at the apex, and separate from one another. This cannot be a matter of doubt to any one who witnesses the spontaneous opening of an antheridium under the microscope. But the structure of the covering layers, even in antheridia, which are still closed, can be fully made out with a good microscope. Gottsche's view may have originated in the circumstance that in Fossombronia, as well as in Anthoceros, the coloured bodies often lie close to the inner side of the wall of the cells of the covering layer, so that the somewhat swollen protuberance of the free outer wall appears to be filled merely with a clear, watery fluid.

With regard to the outer of the two cellular layers of the covering of the antheridia of Haplomitrium, a preparation of which has been figured by Gottsche (l. c., t. xvi, f. 8), I find that the antheridia of this plant are similar to those of Sphaginum; that a thin glassy cuticle encloses the simple covering layer of the antheridia. In Haplomitrium the boundaries of the cells appear upon this cuticle in the form of prominent ridges, but this is not the case in *Sphagnum* (*cymbifolium*). The cells of this covering layer isolate themselves at the time of the ripening of the antheridia of Sphagnum, precisely after the manner of the cells of Haplomitrium; a median lamella of the wall of the cells swells up into a gelatinous substance. By this means the vermiform cells become detached from one another, and separated from the cuticle.

* *l. c.*, vol. xx, p. 294.

CHAPTER IV.

RICCIA AND RIELLA.

The germ-plant of *Riccia glauca* is a simple, short, ribbon-shaped, or three-sided shoot, consisting of homogeneous cellular tissue (Pl. XIII, fig. 1).* The arrangement of the cells of the germ-plant in the direction of the surface corresponds exactly with that in *Pellia epiphylla*. Individual cells of the side edges are transformed into elongated papillæ which are bent forwards; a few cells of the under surface grow out into long, radicular hairs. At an early period there is formed in the middle of the fore edge a deep, narrow indentation, produced by the fact that the growth of the lateral portions of the fore edge exceeds that of the middle (Pl. XIII, fig. 1). In this indentation a new shoot originates. It grows rapidly in length, its fore edge becoming continually wider (Pl. XIII, fig. 2); the wing-shaped lateral portions of the fore edge of the germ-plant are thereby stretched far apart from one another. At the same time the lateral margins of the under part of the new formation amalgamate with that portion of the two wings of the fore edge which is directed inwards. Shortly afterwards new shoots are formed in the angles of both, at the spot where the amalgamation ceases. An almost hemispherical mass of cellular tissue originates at the bottom of the narrow cleft. The arrangement of its few cells repeats in miniature that of the germ-plant (Pl. XIII, fig. 4). On its right and left new shoots are soon produced, clearly originating from the multiplication of a single cell. They amalgamate with the median shoot as soon as their increase in breadth causes their lateral margins to

* I have not been able to procure, under cultivation, the first stages of development of the spores of Riccia or of Anthoceros; in both genera I have been limited to germ-plants which I have found in their native habitats. It is strange that two of the most widely spread and common plants should germinate with so much difficulty.

touch it. The longitudinal growth of the lateral shoots soon surpasses that of the middle shoot, and shortly afterwards the growth of the former in breadth and thickness also exceeds that of the latter. The result is that the median shoot, closely surrounded above and below by the more rapidly growing lateral ones, is pushed to the bottom of one of the narrow crevices formed by the lateral shoots, which shoots are more vigorous in their longitudinal growth. By the multiplication of its cells in the longitudinal direction the median shoot is blended with the two lateral ones, which surround it almost entirely, and far exceed it in size. The shoot formed by the junction of three masses of cells in a state of active longitudinal growth amalgamates at its sides with the advanced portions of the fore edge of the germ-plant by which it is enclosed. On the one side it amalgamates with one of the wing-shaped lateral portions, on the other with the one half of the median shoot, which in the mean time expanding more and more in breadth, has assumed an entirely emarginate shape. By further longitudinal growth the shoots of the second order make their appearance out of the two narrow crevices which the fore edge of the germ-plant exhibits, and which answer to the limits of the median lobe of the fore edge and its lateral portions. The apex of the young Riccia is furcate. The apical point of the bifurcation is the middle of the fore edge of the median shoot. Each point of the fork exhibits in the middle of its fore edge a deep, narrow incision, formed by the two lateral component parts of the shoot of the second order, which almost touch one another. At the base of this incision is the median shoot, of which the apex alone is free, and not united in growth with the lateral ones, and at the sides of which new shoots, being the median ones of the third order, are in process of formation. An active multiplication and expansion of the cells of the median portion of the shoots of the second order now commences; this median portion, by its longitudinal growth and the continually increasing width of its fore edge, pushes asunder the lateral portions of the same shoot which have hitherto confined it in a narrow crevice. New shoots originate in like manner out of its angles. The subsequent ramification of Riccia follows the same

rules; each shoot originates from the blending together of three sub-shoots, and has only a limited growth. New shoots are only formed in the two incisions which the fore edge of each fully developed wedge-shaped shoot exhibits. All shoots, with the exception of the first, which proceeds directly from the spore, undergo complete distortion, caused by the peculiar growth of their median portion and by the expansion of the next younger shoots of a new order, which originate in the incisions of the fore edge of each, and which amalgamate with the median portion; their form passes from a pointed semi-oval, through that of a wedge, to a furcate shape. The repeated furcate ramification of young plants soon renders their entire outline circular.

The multiplication in a longitudinal direction of the cells of each of the three parts of which a shoot is composed takes place through the division of the cells of the fore edge by means of transverse septa inclined to the horizon (Pl. XIII, figs. 7^b, 14). The multiplication is much more active in the median line of the young shoot than at its sides. The cells of the second degree divide by septa almost parallel to the upper and under surface of the shoot, and this division is repeated in the outer of the newly formed cells, by which means the shoot increases in thickness. Immediately after the appearance of the first of the above septa each of the two cells which have originated from the division of each upper cell of the second degree is usually divided into two by the formation of a transverse septum, perpendicular to the outer surface, and cutting the longitudinal axis of the shoot at an angle of 90° (Pl. XIII, fig. 7^b). The cells of the upper half of the flat stem are consequently, even in their earliest stage, usually one half shorter than those of the under half. It is only in those shoots in which the longitudinal growth is especially active that the transverse division of the cells of the under half of the stem lags behind that of those cells of the upper surface which are situated further back from the fore edge (Pl. XIII, figs. 11, 14). Such shoots are usually those which bear the archegonia. The growth in thickness, the division by septa parallel to the surfaces of the shoot, is far more active in those cells which are produced by the

multiplication of the cells of the second degree belonging to the upper surface, than in those which are produced by the multiplication of the like cells of the under surface. The increase in the number of cells, in the direction of the thickness, from the apex of the young shoot backwards, is not unfrequently so rapid that the profile of the shoot appears like a very slightly pointed triangle (Pl. XIII, fig. 11). The continual increase of the breadth of the young shoot during its longitudinal growth takes place by the division of the lateral cells of the fore edge by means of longitudinal septa parallel to the longitudinal axis of the shoot (Pl. XIII, fig. 4). In a more advanced stage of growth, the cells lying nearer the middle of the fore edge also divide by longitudinal septa, slightly diverging from the direction of the median line. The shoot then exhibits a middle row of cells, from which the other cells diverge right and left at different altitudes, like the rays of a fan. The earliest rudiment of each shoot is a simple cell, having a trapezoidal basal outline, situated in the axil of two older shoots (Pl. XIII, fig. 4, *a*); at a little later period many such cells lying near one another are found, in consequence of the commencement of the longitudinal growth, to be already several times transversely divided by inclined septa (Pl. XIII, fig. 4, *b*). The shoot, as it becomes developed, springs forth in the form of a short projection, having its cells arranged in the order already described, from the axil formed by the two older adjoining shoots.

The under side of each joint of the stem of *Riccia glauca* exhibits on each side of the median line small, distichous, obliquely attached leaves, formed of a simple layer of delicate, transparent, cellular tissue (Pl. XIII, fig. 3). They resemble in all their parts those of the Marchantiæ, and, like the latter, are for the most part rapidly destroyed by the bursting forth of hair-like roots. The hollows of the old roots of Riccia, like those of the Marchantiæ, are furnished upon the inner side with very numerous little points projecting inwards (Pl. XIII, fig 4*b*).

On stem-joints which have a tendency to form fruit, individual cells of the upper surface, situated in the angles of the lateral and of the median shoots, protrude out-

wards, and this takes place even during the process of the amalgamation of three shoots into one new shoot (Pl. XIII, fig. 7 *b*). From these cells are developed the organs of fructification, the antheridia or archegonia. The arrangement of these corresponds to the commissures of the three shoots which are uniting to form a single shoot, thus forming two nearly parallel longitudinal rows right and left of the median line. The hemispherical vesicular protuberance which projects above the surface of the young stem-joint divides by a septum inclined to the horizon. In the upper one of the new cells thus formed division immediately takes place by a membrane inclined in the opposite direction (Pl. XIII, figs. 5, 7 *b*). In these phenomena of development the archegonia and antheridia, which originate without any regularity, exactly resemble each other; in their earliest condition they cannot be distinguished from one another.

The cells of the upper side of the young stem which surround the base of the rudiment of an antheridium extend themselves upwards, and thus form a membranous ring which encircles the lower part of the antheridium. This ring usually consists of six cells (Pl. XIII, fig. 10); it is seldom wider. It grows longitudinally by repeated transverse division of the cells of its free upper edge. The sheath thus formed soon overtops the apex of the young, small antheridium (Pl. XIII, figs. 6, 7 *b*); above the antheridium it becomes considerably narrower (Pl. XIII, fig. 9). The upper part of its inner cavity contains a watery fluid; in the lower part, close under the antheridium, air is secreted at an early period, which by careful pressure may be driven out at the narrow mouth of the covering of the antheridium.

The first appearance of the organs of fructification takes place, as is mentioned above, long before the termination of the growth of the stem-joint. The increase in thickness of the surrounding tissue of the surface of the stem nearly keeps pace with the longitudinal growth of the archegonia and of the sharply conical covering of the antheridium, so that the organs of fructification, during their longitudinal development, are continually enclosed in the tissue of the

stem as the latter increases upwards in thickness. In this way the outer side of the covering of the antheridium amalgamates with the adjoining cells of the stem. The contents of these united cells of the antheridum-sheaths become exactly similar to that of the cells of the upper half of the flat stem; numerous chlorophyll-granules are formed in them, and air makes its appearance in the adjoining intercellular spaces. The rudiment of the antheridium, which as yet consists of few cells, has in the mean time considerably increased in size, and become transformed into an oval, cellular body by means of repeated longitudinal and transverse divisions; this oval body consists of a central group of cells, with turbid, mucilaginous contents, surrounded by a layer of tabular cells with watery contents (Pl. XIII, fig. 8). The repeated bisection of the former cells in all three directions leads ultimately to the formation of a spherical mass of numerous, very small, tessellated cells, during the production of which the peripheral layer of tabular cells is gradually entirely displaced (Pl. XIII, fig. 9). The skin-like membrane of the ripening antheridium becomes closely applied to the inner side of the covering of the antheridium, but without growing to it. Each of the small cells produce, during the progress of growth of the antheridium, a small, lenticular vesicle. When the antheridium is ripe the walls of those small cells swell up into a tough jelly, and the outer membrane of the antheridium assumes a delicate, gelatinous consistence.

The amalgamation of the cells of the tissue of the stem with the outer side of the antheridium-sheath does not extend to the young, blunt apex of the latter. Owing to the fact that the longitudinal expansion of its cells first takes place after the complete formation of the stem-joints, this free upper end remains for some time in the form of a rounded, little cone, concealed between the epidermal cells (Pl. XIII, fig. 9). Suddenly the apex elongates itself considerably; by expansion of its cells it often protrudes more than a line above the surface of the stem. The universal expansion of its cells causes a widening of the mouth of the canal which traverses the axis of the sheath, and which leads to the antheridium (Pl. XIII, fig. 10). Through this canal

(according to Bischoff) the contents of the antheridium escape in the form of mucilaginous drops.

In the apical cell of the rudiment of an archegonium division takes place in often-repeated succession by alternately inclined septa. Here, also, the cells of the second degree divide immediately after their formation by radial septa. Immediately after the formation of the radial septum which divides the cell of the second degree, septa parallel to the axis appear in one of the four longitudinal rows of cells of the third degree; these latter septa divide the mother-cells into inner three-sided and outer four-sided cells, so that the organ now consists of a central string of cells, which is surrounded by a single layer of cells arranged in sets of four cells of equal height (Pl. XIII, figs. 12, 13). The apex of the young archegonium swells to a clavate shape; contemporaneously, the basal cell of the central row of cells begins to enlarge its circumference, whereby the base of the archegonium becomes distended (Pl. XIII, fig. 13). The cellular tissue surrounding the archegonia, so far from amalgamating with their outer cellular layer, is often, on the contrary, expanded into a wide cavity surrounding the base of the archegonium (Pl. XIII, fig. 15). The cells of the stem, on the other hand, usually become very closely approximated to the neck of the archegonium, without, however, becoming actually united to it. In comparison with other mosses, the basal cell of the central string of cells becomes considerably enlarged; this takes place, however, at a somewhat later period, shortly before the rupture of the apex of the archegonium. Within the fluid contents of this basal cell there is produced a free spherical cell (Pl. XIII, figs. 14, 15). This grows by degrees, until it fills the mother-cell. There are but few of the Muscales in which this cell is so clearly distinguishable as in Riccia. The remaining cells of the central string are dissolved, and the apex of the archegonium opens. The archegonia, thereupon, either wither, which is a rare occurrence, or a fruit is formed in their ventral portion. The first indication of fruit-formation is the division, by means of an inclined septum, of the free cell which has originated in the

large basal cell of the central string. The upper of the two newly formed cells is then divided by a septum inclined in the opposite direction (Pl. XIII, fig. 16^b). In the apical cell of the now 3-cellular young fruit the division is repeated several times by alternately inclined septa. The cells of the second degree divide by radial longitudinal septa, and the cells thus produced divide into three-sided inner and four-sided outer cells, after the manner of the one row of cells of the third degree belonging to the archegonium. In the four-sided cells, the division is repeated by radial septa, and then by longitudinal septa parallel to the axis of the fruit (Pl. XIII, figs. 17, 18). When the young fruit, which from first to last is almost globular, has attained its full size, the somewhat tabular cells of its upper surface divide by a longitudinal and transverse septum perpendicular to the outer surface, so that the outermost cellular layer of the fruit consists of cells of which the basal outline is four times smaller than that of the inner cells (Pl. XIII, fig. 19).

In each of the latter there ensues a well-defined, gelatinous thickening of the cell-wall (Pl. XIII, fig. 19). Soon afterwards the cells become disconnected by the dissolution of the oldest outermost portion of the cell-wall. The spherical cells thus set free are the mother-cells of the spores. In each of them four special-mother-cells originate, each of which produces a spore. After the individualization of the spores the wall of the half-ripe capsule is absorbed, so that the ripe spores lie free in the cavity of the globular calyptra. This latter is formed by the repeated division into two parts of the cells of the ventral portion of the archegonium, by means of septa perpendicular to the outer surface, such division alternating once with a division by septa parallel to the outer surface. The calyptra of the half-ripe fruit consists of two layers of cells (Pl. XIII, figs. 17, 19); towards the period of maturity the inner one of these disappears. The neck of the archegonium lasts till the fruit is ripe. The cells often assume a beautiful wine-red colour. In rare instances those cells of the impregnated archegonium which lie beneath the central cell of the ventral portion multiply, so that the

form of the organ becomes similar to that of the archegonium of a moss.

Riccia glauca not unfrequently produces gemmæ in the middle of the tissue of the older shoots—small, fleshy masses of cellular tissue, filled with granular mucilage. Their outline resembles that of germ-plants; there is, however, the material distinction that the two lateral portions of the fore edge are not formed at an earlier period than the middle one, or, to speak more accurately, the middle shoot does not, during the formation of the lateral ones, continue in its lowest stage of development, but it forms a prominent, flattened, conical point at the time when the lateral portions begin to protrude themselves. The arrangement of the cells agrees with that of the shoots of perfect plants. Gemmæ which remain long surrounded by the tissue of the stem exhibit the internal disintegration of the tissue which I have figured in Anthoceros and Blasia. The commonest of all liverworts is, strange to say, one of the least known. The numerous investigations and figures of Riccia relate almost exclusively to the organs of fructification (Schmidel, in 'Icones,' t. xliv, xlv; Hedwig, 'Theoria generationis,' ed. ii, 7, 31; Bischoff, 'N. A. A. C. L.,' t. xvii, p. ii, fig. 911 *ff*; Lindenberg's large monograph in vol. xviii of the last-mentioned Proceedings; and lastly, Unger, 'Linnæa,' 1839). The erroneous notion, that a very low state of development of the fruit must be accompanied by an equally low state of development of the vegetative organs, seems to have prevented the accurate investigation of the phenomena of growth in Riccia, which, in comparison with Anthoceros and Pellia, are very complicated. Lindenberg expressly and repeatedly denies to the genus that higher organization, and even the leaves, which he figures most distinctly in very many species. The widely spread notion that the growth of Riccia is radiate, proceeding in all directions from a common median point, may be disproved by the examination of any clod of earth taken from any stubble field in autumn where *Riccia glauca* has begun to germinate.

Riella Reuteri, Mont.—Amongst the various forms of liverworts, Montagne's genus Riella ('Ann. Sc. Nat.,' 3rd.

ser., t. xviii, p. 111; Duriena, l. c., t. i, p. 228; t. ii, p. 50) is the most remarkable, on account of its very peculiar habit. The Algerian *Riella* (*Duriena*) *helicophylla* is the most striking of all; its upright leaf, which is three inches high, and shaped like a winding staircase, being one of the most wonderful of vegetable forms. My investigations of this remarkable genus were made on a species found by Reuter at Geneva, which represents in miniature the vegetative phenomena of the North African species. I am indebted for the materials for my work to the kindness of the discoverer, who sent me numerous living specimens.

Young individuals, whether produced from spores or adventitious shoots (Pl. XIV, figs. 1—4), are formed of short rows of cells, which pass at the fore end into a small, cellular surface. The arrangement of the cells is that which is common to the Ricciæ and the Marchantiæ, viz., in pairs and flabelliform, originating from two cells of the first degree, which are divided alternately by transverse and longitudinal septa. In the young state of the plant there is an excess of formation of transverse septa, nearly at right angles to its median line, and consequently of longitudinal growth. At an early period the multiplication and expansion of the cells of one side of the fore edge considerably exceed that of the other side, so that the punctum vegetationis of the young Riella is turned on one side (Pl. XIV, fig. 2).

Contemporaneously with the appearance of the first leaves, the plant develops a mid-rib, by the production in certain cells of septa parallel to its surfaces; this mid-rib is a strip of massive cellular tissue, consisting sometimes of as many as six layers of cells, which runs along the less highly developed side of the shoot. The rib forms one margin of the flat stem, which may be compared to a stem-joint of Marchantia, of which the membranous left-hand wing has been removed. The helicoid winding of the stem is produced by the lateral twist which takes place in the axis as it grows obliquely upwards, and which is caused by the more rapid development of the left-hand side wing. The twist is always to the right.

Leaves are formed only on the mid-rib. The fraction $2\frac{1}{2}$

represents their arrangement. Each of the surfaces of the plant has two longitudinal rows. The leaf originates from the multiplication of a single cell protruding above the surface of the terminal bud (Pl. XIV, fig. 9). In its early stages, and in those leaves which are nearest to the fore edge of the rib, the successive cell-formation corresponds exactly with that of the scales of ferns. The leaves which lie nearer to the membranous wing are considerably and unsymmetrically developed in breadth in their middle region (Pl. XIV, fig. 8).

The succession of the shoots in Riella, as in the other Ricciæ and Marchantieæ, is pseudo-dichotomous. The first visible ramification takes place usually in the early youth of new individuals, before the appearance of the first leaves. The relation of the two side shoots to the middle principal shoot, of which the development is arrested, and the amalgamation of the latter with the former, may be very easily observed in the simple cellular surface (Pl. XIV, figs. 4, 7^b).

The growth of the antheridia commences by the swelling of a marginal cell of the membranous wing close to the punctum vegetationis, and by the separation of the vesicular protrusion from the original cell-cavity by means of a transverse septum. By the exuberant growth of the cells adjoining its base the rudiment of the antheridium is at once surrounded by a closely-fitting sheath (Pl. XIV, figs. 10, 11). After one or several divisions have taken place in the cell of the first degree by means of transverse septa, and the consequent formation of a short stalk, there occurs in the hemispherical cell a series of divisions coinciding with the like process in Riccia, by which there is produced an oval body consisting of cubical cells, the mother-cells of the spermatozoa, surrounded by a layer of large, flat cells (Pl. XIV, fig. 12). The growing antheridia now appear deeply imbedded in the folds of the membranous wing (Pl. XIV, fig. 13). Antheridia and archegonia are always situated on different shoots. New individuals first produce antheridia. Archegonia usually appear on their shoots of the third, fourth, or fifth degree. The archegonia are situated in the axils of leaves, and are distinguished by a

large, central cell, with comparatively small germinal vesicles (Pl. XIV, figs. 14*a*, *b*).

The base of the young archegonium is surrounded by a small, annular sheath, which, before impregnation, is only from one to four cells in height (Pl. XIV, fig. 14 *b*). After the commencement of the formation of the fruit this sheath grows rapidly into a narrow-mouthed, pitcher-shaped covering, consisting of a single layer of cells (Pl. XIV, figs. 12, 13, 18).

The impregnated germinal vesicle swells at once to the size of the pear-shaped ventral cavity of the archegonium (Pl. XIV, fig. 13), and follows the enlargement of that cavity, which enlargement is caused by the active multiplication of the cells enclosing it. The first division of the primary cell of the fruit takes place by a horizontal septum, which divides the cell into a semi-oval superior, and a filiform inferior, moiety (Pl. XIV, fig. 15). By repeated transverse division the latter becomes the fruit-stalk, consisting of a single row of cells, the lower end of which, at a later period, and by means of divisions caused by septa parallel to the axis, becomes transformed into a clavate, cellular body (Pl. XIV, fig. 18). The upper half becomes the capsule of the fruit; according to the general rule in the Ricciæ and Marchantieæ, it multiplies by repeated divisions of the cells of the first degree by means of septa inclined alternately to the right and to the left (Pl. XIV, fig. 15). After about eight such divisions the capsule becomes globular; its outer layer, the cells of which become tabular, forms the wall. The cells of the interior, becoming loosened and spherical in shape, perfect themselves in different ways. The contents of half of them become turbid from numerous fine granules, and their walls increase in thickness. These are mother-cells, containing in their interior four special-mother-cells, usually arranged in a tetrahedron, from which the spores, which are clothed with a strong, delicately marked episporium, are developed (Pl. XIV, fig. 19). The formation of only two spores in a mother-cell is an irregularity of frequent occurrence. The other cells of the contents of the capsule remain thin-walled,

and starch-granules appear in their interior (Pl. XIV, fig. 19 *b*). They change no further until maturity. This double nature of the cells of the interior of the capsule brings to mind the development of the elaters of the Targionieæ and Marchantieæ. The young conditions of the elaters of the latter answer exactly to the permanent state of those cells of Riella which are intermixed with the spores and contain starch-granules. Riella thus, in more than one point, forms an intermediate link between the Ricciеæ on the one hand, and the Targionieæ and Marchantieæ on the other.

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CHAPTER V.

MARCHANTIEÆ AND TARGIONIEÆ.

Marchantia polymorpha, Fegatella conica, Rebouillia hemispherica, Lunularia vulgaris. Targionia hypophylla.

THE growth of the Marchantieæ and Targonieæ resembles in its principal phenomena that of Pellia, Riccia, and Anthoceros. The essential circumstance, viz., the origin of each new shoot by the amalgamation of three shoots, which are developed in one of the two indentations of the fore edge of an older shoot, is in these plants, especially in the genera Lunularia and Fegatella, more clearly marked than in any others.*

The vegetative organs of *Marchantia polymorpha, Fegatella conica, Rebouillia hemispherica, Lunularia vulgaris*, and *Targionia hypophylla* exhibit great similarity in development

* The rudiments of those shoots of *Fegatalla conica* which are to be developed in the early spring originate in the preceding October; on the right and left of a nearly hemispherical mass of cellular tissue, situated at the bottom of one of the two indentations of the fore edge of the fully developed shoot of the next higher order, there are formed two smaller, almost conical shoots, which, by amalgamating with the one between them, form the bud of the new shoot. The shoot grows slowly in a longitudinal direction until the commencement of winter; the fore edge of the median shoot becomes, at the same time, continually wider (Pl. XVI, fig. 1, middle of November). After the coldest months are over, there is formed on either side of the median lobe the rudiment of a new shoot, which has already attained a tolerably perfect condition at the time when the longitudinal expansion of the oldest hinder cells of the shoot formed at the commencement of winter begins to cause the latter to protrude out of the indentation of the edge of the stem-joint of the previous year. The shoot whose longitudinal expansion commences, appears at this time as if bent upwards; a thick-fleshed, small mass of cellular tissue, already slightly furcate at the fore edge by the commencement of the longitudinal development of the shoots of a new order. The lateral margins of the shoot are bent strongly inwards, and it is closely folded together in its median line.

and structure. The longitudinal growth of each shoot is caused by repeated division in its apical cells, by means of alternately inclined septa (Lunularia, Pl. XV, fig. 19; Fegatella, Pl. XVI, fig. 3). Soon after the first division of this kind has taken place in the mother-cell of a new shoot (which mother-cell lies at the bottom of the axil of two older shoots), the number of the apical cells is doubled by the appearance of a longitudinal septum (Pl. XVI, fig. 2). The fore edge of the shoot widens continually during and until the cessation of its longitudinal development, by means of repeated division of the apical cells by longitudinal septa; this increase in breadth is more or less rapid, according to the circumstances under which the plant is growing, and according to the species of plant. The differences in habit in different species, as well as in individuals of the same species growing under different circumstances, depend, in the first place, upon whether the lateral margins of the new shoots amalgamate with the adjoining lobes of the fore edge for a considerable length, or not. Those shoots of Fegatella and of Rebouillia which are formed late in autumn, which remain quiescent during the coldest part of the year, and develope themselves in early spring, remain completely separated from the projecting portions of the shoots of the previous year; this is the cause of the jointed appearance of the leaf-like stem of these species. In Marchantia, in Targionia under all circumstances, and in the summer shoots of Fegatella and Rebouillia, the amalgamation is, on the other hand, very complete. In the next place, differences of habit depend also upon the length of the lines of amalgamation of the three shoots which combine to form one shoot. In Fegatella, and in specimens of *Marchantia polymorpha* and *Lunularia vulgaris*, which grow in very moist places, the amalgamation is far more considerable than in specimens of the same species from dry habitats,* or than

* The length of the amalgamation is manifestly to be measured by the number of cells, and not by lines and inches. The expansion of individual cells has the greatest influence upon the absolute length of the shoots. The latter becomes quite enormous when new shoots of *Marchantia polymorpha*, covered by older portions of the mother-plants, are making their way to the light.

is the case in Rebouillia and Targionia. Differences of habit depend also upon the greater or less rapidity of the expansion of the fore edge of the shoots during their longitudinal growth, and, lastly, upon the fact whether the older shoots die and moulder away with greater or less rapidity. In *Rebouillia hemispherica* and *Fegatella conica* they last for several years; in Targionia and Marchantia the decay of the older generation of shoots begins very shortly after the complete formation of the next youngest shoots. It often happens that almost every trace of the (pseudo) furcate ramification of the plant is obliterated by the fact of a new shoot being developed in one only of the indentations of the fore edge of an older shoot, the other new shoot, situated in the other indentation, becoming abortive. This is often the case in Rebouillia and Targionia. The buds (bulbils according to Mirbel) of Lunularia and Marchantia, which are formed in special receptacles on the median line of the shoots, afford a particularly striking example of the above species of ramification. These receptacles are formed in the following manner:—in the earliest stage of the shoot, cell-multiplication commences, either all round the spot where the buds are destined to be formed, or in a semicircular chain of cells (the semicircle lying open to the front) of the upper side of the shoot. This cell-multiplication gives rise in Marchantia to an annular, in Lunularia to a horse-shoe shaped cushion. The division by septa parallel to the surface, of those cells of the upper side of the shoot which are enclosed by the cushion, soon ceases, whilst it continues for some time in the cells lying outside. Thus the space of the upper surface which is enclosed by the cellular rampart, and is destined to form gemmæ, becomes a depression. The margin of the wall grows in Lunularia into a delicate membrane (Pl. XV, fig. 19), consisting of a single layer of cells. In Marchantia from sixteen to twenty teeth sprout from it (Pl. XV, figs. 1, 1^b), which incline towards one another when young, and thus cover the gemmæ; afterwards they become upright. The history of the development of these teeth is as follows:—every other cell of the edge of the annular wall expands considerably outwards.

The protruding portion is separated by a transverse septum from the rest of the cavity of the cell, which is then divided by a longitudinal septum. The cells which are elevated above the margin of the wall are transformed into flat teeth, consisting of a single row of cells, resulting from a division by transverse septa, which is continually repeated in each apical cell (Pl. XV, fig. 1^b). Repeated division takes place in the interstitial cells by means of longitudinal septa perpendicular to the broader surface; and by this division, which begins at the base and progresses to the apex with increasing intensity, the teeth, at a later period, increase in breadth. At the same time the circumference of the annular wall of the bud-receptacle increases, through the division of its cells by means of longitudinal septa. At the points of origin of the teeth this latter increase corresponds with the expansion of the teeth; underneath it is much less. By this means the form of the edge of the bud-receptacle becomes that of a cup.

Some time before the appearance of the marginal teeth the formation of the first gemmæ commences. Individual cells of the base of the receptacle produce a papilla upon the middle point of their free upper wall (Pl. XV, fig. 1^b). This papilla is soon separated by a transverse septum from the rest of the cell-cavity. The new semi-oval cell, after previous longitudinal expansion, is divided by a transverse septum (Pl. XV, fig. 1^b). The lower one of the cells thus produced is the stalk, the other the mother-cell of the gemma. The latter increases considerably in breadth, and by means of transverse division, which is always repeated twice in the terminal cell, it becomes transformed into a row of four short, wide, and low cells. Each of them divides by a longitudinal septum (Pl. XV, fig. 2). The three lower pairs of cells thus formed are divided by septa parallel to the last-mentioned septum; the lower pair once, the two higher pairs twice. The repetitions of the division occur, as is usual in similar cases, always in the outer cells. Each of the two apical cells of the bud, on the other hand, divide by septa having a strong lateral inclination, into an inner and an outer cell, the former having a trapezoidal, and the latter a triangular basal, outline. The former is

soon divided by a septum at right angles to the longitudinal line of the bud. The latter cell, after previous transverse expansion, divides by a septum parallel to the chord of the arc represented by that portion of the margin of the bud to which the cell in question belongs. The outer ones of the newly formed cells then divide by septa at right angles with the last-formed septum (Pl. XV, figs. 3—5; and compare Nägeli's excellent account of this process, 'Zeitschr. f. Bot.,' Hft. 2, S. 150). The further increase in the cells of the bud is caused by the growth of septa in the cells of its fore edge alternately at right angles or parallel to its margin, and by the formation of septa parallel to the margin in the cells of the edge of its lower part. The increase in breadth of the apex exceeds, at an early period, that of the base (Pl. XV, figs. 3, 4).

The longitudinal growth of the bud is limited, as is the case with all the shoots of the Marchantieæ. When it is finished a very considerable increase in the breadth of the lower part of the bud commences. Here the marginal cells divide repeatedly by septa parallel to the margin, alternating with radial septa. The marginal cells also of the upper part, with the exception of those of the apex, multiply in like manner, although less actively; they are soon overtaken by those of the lower part. The cells, however, of those two places on the lateral margins at which, at an earlier period, the upper, wider half of the bud separated itself from the lower, narrower portion, take no part whatever in this multiplication (Pl. XV, fig. 7), and as little also in the important expansion in length and breadth which occurs shortly afterwards in the remaining cells of the buds. In this way two very deep, lateral indentations are produced in the middle of the buds, the innermost space of which indentations is occupied by a group of small cells, with a trapezoidal basal outline (Pl. XV, figs. 7, 8). At the time when as many as ten cells can be counted in the longitudinal line of the bud, this group appears as a single layer of cells. Then, for the first time, it begins to grow in thickness; in the first place, by the division of the cells of the middle region by horizontal septa (Pl. XV, fig. 1^b). For a still longer period the lon-

gitudinal growth of the bud is produced exclusively by division of the apical cells, by means of septa at right angles to the surfaces of the bud; the transverse septa which appear in the apical cells are strictly vertical; the fore edge of the bud is a simple cellular layer. Afterwards, for the first time, when the middle-region has become more and more thickened by the repeated formation of septa parallel to the surface, and when this thickening has advanced close to the fore edge, the transverse septa appear in the apical cells, inclined alternately upwards and downwards, and parallel to the circumference of the bud. Thus the form of longitudinal growth of the bud passes into that which occurs in the shoots of older plants.

The arrangement of the buds of Lunularia and of Marchantia, with respect to the longitudinal axis of the shoot upon which they originate, is a very constant one; their surfaces are always at right angles to that axis (Pl. XV, figs. 1^b, 19). Until their longitudinal growth is almost completed, the buds are surrounded by a transparent gelatinous mucilage. When the growth of the bud in length and breadth is ended, the cell which supports it dies and withers, and the bud becomes free. A moist substratum outside the receptacle is all that is now necessary for its further development.

Under such circumstances some of the cells of its under side first grow out into rootlets. Then new shoots begin to be developed from the bottom of the lateral indentations of the bud. The middle cell of the group which has been so long arrested in its growth, and which is somewhat larger than its neighbours, becomes the mother-cell of the first new shoot (Pl. XV, fig. 8). It divides by a transverse septum, and the front one of the new cells by a longitudinal septum. The division of the latter by laterally inclined septa causes the further growth of the shoot, which proceeds precisely in the same manner as that in which the new shoots of *Pellia epiphylla* develope themselves, with this difference only, that the transverse divisions of the apical cells are always produced by means of septa inclined to the horizon in alternate directions. The lateral margins of the young shoots thus formed amalgamate

for a considerable extent with those of the indentation of the bud. The cells which have amalgamated expand considerably in length, and to some extent in breadth. When a shoot is formed in each of the two lateral indentations the bud becomes developed into a wide band, on one side of which may be seen the spot at which the bud was attached to the cell which bore it, and which spot is conspicuous from its brown colour, and by the arrangement of the cells by which it is surrounded. This is the case in *Marchantia polymorpha* (Pl. XV, fig. 9). In *Lunularia vulgaris*, on the other hand, it is a rule almost without exception that a shoot is developed only on one side of the bud, the shoot on the other side becoming abortive. Here the bud in its further growth, assumes the form of a disc drawn out in breadth, and having an indentation on one side. On the other side it sends out a long band, constricted at the fore edge, and on a third side the primary place of attachment is still visible (Pl. XV, fig. 20).

On both sides of the new shoot, and in the angles which it forms with the prominent portions of the lateral margin of the bud, two new cellular masses are formed which are capable of development—in the first place a median, and then two lateral shoots. The shoot composed of the three amalgamated shoots unites by its lateral margins with those portions of the next oldest shoot which adjoin it on the right hand and on the left, and it soon makes its appearance out of the indentation, in the form of a flat mass of cellular tissue, having two notches at the fore edge, and becoming wider in front.

A second form of growth, in which the shoots make their appearance in irregular positions, occurs occasionally in Lunularia and Marchantia, and more frequently in Targionia, Rebouillia, and Fegatella. A process of cell-multiplication commences in individual cells (usually near the median line) of the under side of perfect shoots, by means of which slender, delicate shoots are produced, which soon throw out rootlets, and which, by the decay of their posterior parts, separate from the mother-plant and become independent individuals. They exhibit exactly the

same arrangement of the cells as the vigorous normal shoots of the mother-plant; this may be observed most clearly in *Fegatella conica*. The mode of ramification of this second form of bud agrees with that of germ-plants; the fore edge widens considerably, the lateral portions grow more vigorously than the median point, and from the latter a new shoot protrudes, at whose sides the shoots of a new order originate. This process differs materially from the development of the bulbils. There is here the same difference as exists between the development of the germ-plants and the buds of Riccia.

The leaves of the Marchantieæ are delicate lamellæ of cellular tissue, closely pressed to the under side of the flat stem. In an advanced state they sometimes exhibit at the base a double layer of cells containing a small quantity of chlorophyll, the remainder consisting of a single layer of hyaline cells. They develope themselves in a backward direction, towards the place where three shoots unite to form one shoot, and are situated on the under side of the shoot, in two rows parallel to its longitudinal axis, arranged according to the fraction $\frac{1}{2}$. The first rudiments of the leaf are formed as follows:—one of the cells of the under side of the stem protrudes outwardly, and the protuberance becomes divided from the original cell-cavity by a transverse septum (Pl. XVI, fig. 15). At this time the stem is but little developed in breadth, and is almost semicircular in a transverse section. The rudiment of the leaf increases in length by repeated transverse division of its apical cell. The cells of the second degree are divided by longitudinal septa (Pl. XVI, figs. 15, 16). In *Fegatella conica* this division, even in the youngest stage of the leaf, extends as far as the apical cell; the leaf, when only four cells in height, appears to consist of a short, double row of flat cells (Pl. XVI, fig. 11). The three pairs of interstitial cells divide by septa parallel to the margin, and the two apical cells by septa inclined somewhat laterally. The two inner ones of the four cells which at this period constitute the fore edge of the young leaf are now divided by transverse septa, and the four cells thus formed by longitudinal septa (Pl. XVI, fig. 12). The outline of the leaf then becomes

rounded by a process of cell-formation which appears very similar to that by which the cells of the very young gemmæ of Marchantia increase in breadth (Pl. XVI, fig. 13). The cell-multiplication on the side of the leaf furthest from the median line of the shoot soon exceeds that of the other side, causing the one-sided appearance which is usual in the leaves of Marchantia. The cell-multiplication is arrested at the apex, whilst it continues at the base. Many of the marginal cells grow into crooked, short, bicellular, clavate hairs, similar to those which are found close under the fore edge of rapidly growing shoots of Pellia, as well as in the young parts of many other Jungermanniæ. Individual cells, arranged at definite distances on the margin, multiply for a longer period than their neighbours, by which means the leaf soon becomes angular.

The development of the leaves of Targionia, Rebouillia, Lunularia, and Marchantia, appears not to differ essentially from the above. In *Marchantia polymorpha* even the leaves exhibit the tendency, common in these plants, of sending out from the margins of their vegetative organs dentate, chaffy processes, a tendency which is seen on the marginal scales on the edges of the bud-receptacles on the perichæte and perigone. By these processes the leaves are beautifully fringed.

The well known characteristic structure of the flat stem of the Marchantieæ is marked by the separation of the tissue of the stem into—first, an inferior layer of large, very elongated cells, without intercellular spaces;—secondly, a layer superimposed upon the latter layer, and consisting of moniliform rows of cells, separated by wide air-cavities and rich in chlorophyll, which layer is divided into partitions by rhomboidal, cellular walls, each consisting of a single stratum;—and, lastly, an epidermis with transparent cell-contents, covering the latter layer, which is in close connexion only with the cellular walls just mentioned, and is pierced by a stomate of peculiar structure at the middle point of each of the partitions of the underlying layer. The foundation of this peculiar structure is laid at a very early period. At a little distance behind the punctum vegetationis of

the very young shoot, long before the completion of its growth in thickness, air-cavities are formed just under the upper surface, separated from it only by a single layer of cells (Pl. XV, fig. 21; Pl. XVI, fig. 3). The portions of tissue between the air-cavities form a network of single rows of cells. As these cells continue to divide by septa parallel to the surface of the stem, the lid of the air-cavities is carried upwards. The base of the cavities is quite flat. Lastly, after repeated previous bipartition of the cells of the base, by means of vertical septa placed crosswise, the latter cells protrude upwards (Pl. XV, fig. 21), and by repeated transverse division are quickly transformed into the moniliform chains of cells which, when the shoot is perfected, are pressed closely to one another and fill up the air-cavities.

The epidermal cell which is situated over the middle of each air-cavity separates by repeated bipartition into four (Marchantia), six (Fegatella, Pl. XVI, fig. 4), or more (Rebouillia) three-sided cells arranged in a circle. In the centre of the circle the cells part from one another; a polyhedral opening is formed, the circumference of which, owing to the expansion in a tangential direction of the surrounding cells, is often considerable, and through which the air-cavities, in which air is secreted at an early period, comes into contact with the atmosphere. The first development of the stomata of the Marchantieæ is only distinguished from that of higher plants by the fact that more than one bipartition of the mother-cell precedes the opening of the commissure of the cells which form the boundary of the opening.

The cells, from four to eight in number, which surround the stomata of the Marchanticæ divide, during the expansion of the stem to which they belong, by means of septa parallel to the small side walls; this often occurs repeatedly, so that a hollow arch, with a perforated apex, is formed over the middle point of the air-cavity. The outer walls of the circular, wart-like protuberance of the epidermis divide also by radial septa.

The inflorescence of a Marchantia owes its origin to the

preponderating development in thickness and length, and the proportionally small development in breadth, of the median component of the last vegetative shoot. In its earliest youth it exhibits a hemispherical, and at a somewhat later period a cylindrical, mass of fleshy, cellular tissue, with a bluntly rounded apex (Pl. XVI, fig. 5; Pl. XI, fig. 10). Its longitudinal growth results, as is the case in vegetative shoots, from repeated division of the apical cell by means of alternately inclined septa, except that at the first commencement of the formation of the inflorescence no more than one apical cell is present (Pl. XVI, fig. 5). During the further development there is formed on its under side a deep channel, which is (Pl. XVI, fig. 7) destined to receive the rootlets which are produced at a later period by the upper pileate portion, into which the apex of the young rudiment of the head of the fruit is transformed by means of active growth in the direction of its breadth. The under side of the stem of some species (*Marchantia polymorpha*, Pl. XVI, fig. 17, for instance) exhibits two such channels. In both cases the channels appear to originate in an active multiplication of the cells of the inverted sides of the stem of the receptacle. The rootlets first appear from the lower end of the channel, and penetrate into the ground.

The shoot which produces the inflorescence bears numerous narrow, scattered leaves, in which the apex always consists of one cell and the base of (at the most) a few cells. The leaves are not produced on the apical portion, which eventually forms the fruit. It may often be observed that the cells of the base in these leaves multiply for a much longer period than those of the apex.

The lateral portions of the undermost oldest parts of the common stem of *Rebouillia hemispherica* extend considerably forwards; they close together so as to form a very narrow, linear fissure in front of the transversely oval channel, and they amalgamate with the prominent lateral portions of the fore edge of the shoot upon which the fruit-stem is situated. The outer surface bears connivent leaves above the apex of the rudiment of the inflorescence. The longitudinal channel of the under side of the fruit-stem does

not reach quite to its base; it projects in the form of a blunt knob into the indentation of the fore edge of the last vegetative shoot (Pl. XII, fig. 17).

The differentiation of the tissue of the leafy, expanded, vegetative shoots is not continued into the stem of the fructifying shoot. At the point where it is attached to the next older shoot the upper side of the stem decreases by a steep inclination to the extent of the height of the layer which bears the air-cavities (Pl. XV, fig. 12; Pl. XVI, fig. 17).

The archegonia spring from the lateral margins of the receptacle in the form of cylinders of cellular tissue directed obliquely upwards (Pl. XV, fig. 6). The essential features of their development and structure correspond with those of the Jungermanniæ and the mosses. Very soon after the appearance of the archegonia the portion of the receptacle above them begins to grow considerably in breadth, and also downwards. The archegonia, in consequence, appear shortly afterwards to be situated on the under side of the expanded receptacle (Pl. XV, fig. 11; Pl. XVI, fig. 7). The receptacle of *Rebouilla hemispherica* usually produces only four archegonia; sometimes one more, frequently less. The cells of the upper surface of the ventral portion of the archegonium divide at an early period by septa parallel to the axis; even before the bursting of the apex the central cell is surrounded by a double layer of cells (Pl. XVI, fig. 17). The neck is considerably bent upwards. The expansion of the receptacle above the archegonia takes place at a late period compared with the other Marchanticæ, *i. e.* not till after the opening of the apices of the archegonia. The growth of the margin of the receptacle downwards is at first more vigorous *between* the archegonia than *above* them.

In the neighbourhood of impregnated archegonia these circumstances are altered. The tissue of the receptacle *above* them increases in mass not less actively than in their neighbourhood. A fleshy sheath is formed, encircling the fore part and sides of the swollen ventral portion of the archegonium. Behind the young calyptra also the margins of the sheath approximate to one another, so as to form a narrow fissure; the bent neck only of the archegonium projects out

of the narrow covering which is closely attached to the calyptra (Pl. XVI, fig. 20). Viewed from the outside, these processes of the receptacle appear like fleshy appendages of its margin. The number of them is the same as that of the impregnated archegonia, viz., from one to five. (See Bischoff's figures, 'N. A. A. C. L.,' vol. xvii, part 2, pl. 49, figs. 1—4.)

The tendency of the ventral portion of the archegonium of Rebouillia to develope itself largely is especially remarkable in archegonia just impregnated. Here the multiplication of the cells near the central cell is so rapid that the latter becomes a wide, flask-shaped cavity, even before the occurrence of the first division of the germinal vesicle contained in its interior. This elongated, ellipsoidal cell lies free in the cavity, entirely imbedded in transparent mucilage (Pl. XVII, fig. 18).

The fruit-rudiment in Rebouillia, like that of Riccia, Targionia, Marchantia, and Fegatella, exhibits the remarkable species of growth which occurs in the fruit of mosses, although, in other respects, the plants just mentioned are nearer to the Jungermanniæ than to the mosses. This growth consists in the division of the mother-cell by a strongly inclined septum, and a continually repeated division of the apical cell of the fruit-rudiment by means of septa inclined alternately in two directions. The form of the young fruit-rudiment is very slender (Pl. XVI, fig. 19); it is only a double row of elongated cells. The longitudinal growth, however, soon ends; a considerable multiplication of the cells commences in a diametrical direction, a multiplication which is more active at the apex (the future capsule) and at the base (the growing knobby enlargement) than in the middle (the future fruit-stalk). The increase in the size of the fruit is so considerable at the approach of maturity that it usually entirely destroys the upper part of the calyptra; it then lies naked in the fleshy sheath formed by the growth of the margin of the receptacle. *Fegatella conica* developes from six to eight archegonia on the lateral margins of its receptacle (Pl. XVI, fig. 6). These archegonia are, at an early period, surrounded by the receptacle, which is growing rapidly in breadth. The mass

of the receptacle increases very considerably round the base of each archegonium, so that these soon have the appearance of deep, almost cylindrical, cavities, sunk in the under side of the receptacle (Pl. XVII, figs. 7, 8). The fructification consists, as it were, of as many amalgamated cornet-shaped masses of cellular tissue as there are archegonia. The very considerable expansion of the cells of these masses causes their margins, in half-developed receptacles, to extend close to the point of origin of the common fruit-stalk.

The archegonia of Fegatella resemble those of Rebouillia in the early and extensive development of their ventral portion. Like the great number of liverworts whose archegonia have to live through the winter, they exhibit the early duplication of the cellular layer surrounding the central cell of the ventral portion, and the extensive growth in thickness of the wall of the young calyptra after the occurrence of impregnation (Pl. XVI, fig. 8). The neck is proportionately long.

The rudimentary fruit, when consisting only of a few cells, may be very easily detached (Pl. XVI, fig. 9). The ladder-like arrangement of its cells, caused by the repeated division of an apical cell by means of alternately inclined septa, is uncommonly sharply defined. The growth of the uppermost part of the young fruit in thickness, *i. e.* the foundation of the capsule, commences at a very early period (Pl. XVI, fig. 10). The lower portion of the fruit-stem is very slightly developed; the formation of a knotty enlargement of its base is entirely suppressed. As observed by Schmidel ('Icones plant.,' p. 121) and Bischoff, the stem detaches itself spontaneously when the fruit is ripe from the tissue in which it is inserted. The first archegonia of *Marchantia polymorpha* appear in like manner at the margin of the young receptacle, usually eight in number, placed at regular distances. Those at the hinder part of the receptacle (*i. e.* turned away from the fore edge of the plant) are developed, as in Rebouillia and Fegatella, much earlier than those on the opposite part (Pl. XV, figs. 11, 12). Very soon after the appearance of the first archegonia new ones are formed on the under side of the pileate receptacle,

and nearer to its centre, arranged in radial double rows (Pl. XV, fig. 11). A phenomenon, of which traces are seen in Rebouillia, is very strongly marked in Marchantia: the underside of the margin of the receptacle is developed at a very early period between each two archegonia into a process extending downwards for a considerable distance, whose form gradually passes from that of a hemispherical wart to that of a long, cylindrical prolongation, curved slightly inwards, with deep, longitudinal furrows on the under side, in which rootlets lie concealed.

The archegonia of *Marchantia polymorpha* are large-celled, the ventral portion being remarkably swollen at an early period. A single layer of flat, tabular cells surrounds the proportionably large central cell of the ventral portion, which is attached almost immediately to the under side of the receptacle. The neck of the archegonium, which in its earliest youth is curved strongly upwards (Pl. XV, fig. 12), is pointed directly downwards at the time when the apex opens (Pl. XV, figs. 13, 14).

After the parting asunder of the cells of the apex, the central cell of the ventral portion of the impregnated archegonium enlarges very considerably. A free, oval cell entirely fills its inner cavity. Its large central nucleus is very plainly distinguishable as a clear vesicle in the thick granular mucilage (Pl. XV, figs. 13, 14). The transformation of this cell into the rudimentary fruit is introduced by the appearance of a much inclined longitudinal septum Pl. XV, fig. 15). The septa, which are formed at a later period in the apical cell, diverge only very slightly from the longitudinal axis of the fruit. I have but seldom and only imperfectly succeeded in detaching the young rudimentary fruit. It remains for some time spherical; its cells soon become very small by repeated cell-divisions.

After the first divisions of the primary cell of the rudimentary fruit, the cells of the young calyptra double themselves by the formation of septa parallel to the outer surface. A special covering has at an earlier period been formed close round each impregnated archegonium. The ring of bells of the under side of the receptacle which surrounds the case of the archegonium protrudes outwards; the protru-

ding portions are separated from the original cell-cavity by transverse septa (Pl. XV, fig. 13). By repeated transverse divisions of the apical cells of the membranous sheath, produced by septa parallel to the free margin, the young covering grows in length (Pl. XV, fig. 14). Its further development, viz., the transformation of the cylindrical shape into that of a distended pitcher (Pl. XV, fig. 15), corresponds to that of the covering of *Frullania dilatata*.

Close under the arched upper surface of the receptacle of Marchantia, including the outer surfaces of the upward-growing shoots of the lateral margin, numerous air-cavities are formed, even before the first appearance of the archegonia. They are formed in the same manner as the air-cavities of the stem. At the first appearance of the air-cavity one epidermal cell only detaches itself from the underlying tissue of the receptacle (Pl. XVI, fig. 17, underneath, to the right). By repeated transverse division of the mural rows of cells lying between the air-cavities, the lid of the cavity is carried rapidly upwards. This epidermal cell, which closes the air-cavity, forms itself into a stomate. It divides by a septum perpendicular to the outer surface, as is the case in the first stage of the stomata of the upper side of vegetative shoots; both daughter-cells then divide by a septum at right angles to the one last formed (Pl. XVI, fig. 17, in the middle). The four cells part asunder at their edges of contact, and the air-cavities come into connexion with the outward air. The four cells of which the young stomate now consists divide repeatedly by transverse septa. The first partitions thus formed are parallel to the upper side of the receptacle; the later ones, which are produced in the upper and under of the newly formed cells, are strongly inclined either towards or away from the passage which traverses the axis of the stomate. The apex of the organ protrudes above the upper side of the receptacle in the form of a conical wart, open at the apex; the base lies deep down in the air-cavity (Pl. XVI, fig. 7). The middle part of the canal, which traverses the stomate, is strongly distended. In the mean time the apical cells of the cellular walls, which separated

the individual air-cavities from one another, have also multiplied considerably. A remarkable transverse expansion has preceded the repeated bipartitions (Pl. XVI, fig. 17, at the bottom, on the left side); the sides of the cells are at an early period forced above the air-cavity, to which they are contiguous. The process of the production of those cells of the epidermis of the receptacle, which are in connexion with the cellular layers separating the air-cavities, consequently soon helps to form the lid of those cavities, which at an earlier stage was represented only by the young stomate or its mother-cell.

The base of the side walls of the air-cavities of Marchantia soon produce moniliform chains of cells filled with chlorophyll. In Rebouillia most of the cells of those walls do not usually do more than project considerably, but individual cells grow out into short, cellular rows. The walls of the air-cavities of the receptacle of Fegatella remain for a very long time smooth and even.

The median component part of the fructifying shoot of *Targionia hypophylla* does not become changed into a specially formed receptacle, but developes the archegonia at once, the latter being from one to five in number (Pl. XV, fig. 21). The lower half of the archegonia is pressed into the exceedingly narrow fissure, within which the lateral wings of the fore edge of the fertile shoot confine the rudimentary median part. The necks of the archegonia, which are bent upwards, project from the fissure into space. A considerable increase of the parts of the tissue adjoining the archegonia in front commences even during the longitudinal growth of the latter. At the junction of the median shoot with the lateral wings of the fore edge, above the point of attachment of the archegonia, the cellular layers expand and multiply vigorously in a longitudinal direction; their thickness is proportionate to the development of the layer of air-cavities. Before the apices of the archegonia open, a flat covering is formed, which exceeds the archegonia in height, and which unites the approximated lateral portions of the fore edge into one surface. The separation of the upper side of the stem into the layer of air-cavities and the epidermal layer takes

place within this covering (Pl. XV, fig. 21). At the same time broad, fleshy, cellular masses, concave above and within, rise out of the angles between the median shoot (which bears the archegonia) and the lateral wings. They amalgamate with one another, and by their upper margin they unite with the above-mentioned covering. Thus, there is formed a blunt, triangular envelope, enclosing the lower part of the archegonia, from the narrow three-sided opening of which the apices of the unimpregnated archegonia protrude (Pl. XV, fig. 21). The rather thin walls of the envelope, which are turned downwards, consist of homogeneous cellular tissue.

When a rudimentary fruit is formed in an archegonium the envelope enlarges with wonderful rapidity, especially by expansion of its cells. It very soon entirely encloses the impregnated archegonium. The cells adjoining the mouth, which continues very narrow, grow out into short papillæ.

The archegonia are slender, almost cylindrical. The cropped appearance of the apex, which occurs also in the archegonia of the Marchantieæ, is seen with remarkable distinctness (Pl. XV, figs. 22, 23). The cells of the ventral portion double themselves at an early period by septa parallel to the circumference. The inner cells adjoining the central cell become filled with granular matter, as in Pellia (Pl. XV, fig. 22). Immediately after impregnation the cells of the incipient calyptra multiply very rapidly, so that, as in Rebouillia, the central cell becomes a fusiform cavity, in which the mother-cell of the rudimentary fruit lies free (Pl. XV, fig. 22).

The rudimentary fruit in its earliest youth is narrowly spindle-shaped, composed of two double rows of cells (Pl. XV, fig. 24, detached; fig. 23, enclosed by the calyptra). The growth in thickness begins much earlier at the upper end than at the lower (Pl. XV, figs. 23, 25). The latter penetrates deeply into the tissue of that portion of the stem which bears the impregnated archegonium, and which has become transformed by active and repeated division of its cells into a conical, cellular mass. The lower end of the rudimentary fruit, which is originally of a pointed, conical form, changes gradually into a spherical enlargement by trans-

verse expansion and subsequent repeated bipartition of the cells of its circumference (Pl. XV, fig. 26).

The arrangement of the spore-mother-cells and of the elaters in Targionia, and also, it would seem, in the Marchantieæ, is very much the same as in *Fossombronia pusilla*. At the time of the differentiation of the two kinds of contents of the capsule, the cells destined to form the elaters are hardly perceptibly longer and thinner than the future mother-cells of the spores (Pl. XV, fig. 29). The elaters and spore-mother-cells lie across one another somewhat like the chlorophyll-cells and the air-cells of the leaf of Sphagnum. A remarkable longitudinal expansion of the elaters first occurs when the prominences of the inner wall of the spore-mother-cell begin to be seen (Pl. XV, fig. 30).

The antheridia of the Marchantieæ are, as is well known, united in large numbers on the upper side of peculiarly formed shoots, and enclosed in flask-shaped cavities of the tissue.

The first stage of development of these shoots in *Marchantia polymorpha* exactly resembles the first rudiments of the head of the inflorescence. Here as there the forward, upper portion of the narrow, almost cylindrical shoot becomes developed considerably in breadth, protruding beyond the lower, stem-like portion, like the pileus of a fungus. A number of cells of the upper side of this disc, which is slightly convex above and strongly so beneath, protrude outwards in the form of papillæ; between them the epidermis detaches itself from the underlying tissue. The shortly cylindrical cellular processes, the first rudiments of the antheridia, are outgrown by the cells surrounding them, and are sunk down into circular cavities of the upper surface. This arises from the rapid multiplication of the cells of the circle which bears the detached fragments of the epidermis, which multiplication is caused by rapid and frequently repeated division of these cells by means of septa parallel to the surface of the antheridial disc (Pl. XV, fig. 16). The above process commences in the middle point of the young antheridial disc, and progresses from thence to its growing margin.

The mother-cell of the antheridium assumes the form of

an elongated, oval cellular mass, consisting of four rows of cells (Pl. XV, fig. 16). This arises from frequently repeated division of the apical cell by means of alternately inclined septa, and by the production of radial longitudinal septa in the cells of the second degree. The cells of one of these rows, with the exception of the two at the base, and the one next to the apex, divide by septa parallel to the longitudinal axis of the antheridium, and cutting the side walls of the mother-cells at an angle of 45°. The antheridium now consists of a short, central string of cells, surrounded by a single layer, the cells of which are arranged in successive sets of four cells of equal height. The further development, like the preceding, corresponds with that of the antheridium of Anthoceros and Pellia, with this distinction, that the multiplication of the cells in the direction of the longitudinal axis, exceeds that in the direction of the thickness. The ripe antheridium is oval.

The apices of the cellular masses which arise between the antheridia expand considerably in breadth as soon as they have outgrown the antheridia. They consequently soon close together over the antheridium, so as to form narrow passages, hardly perceptible from the outside. The cell which covers the air-cavity develops itself into a stomate, exactly in the same way as the median cell of the covering of the air-cavities on the upper side of the receptacle (Pl. XV, fig. 16). The cells adjoining this cell divide by slightly inclined longitudinal septa parallel to the axis of the stomate. The inner of the cells thus produced, which form a ring round the stomate, take part in the formation of the covering of the air-cavity, expanding at the same time in breadth. In the air-cavities in the middle of the antheridial disc these cells divide frequently by longitudinal and transverse septa perpendicular to the outer surface. The cells of the base of the disc grow into the expanding air-cavities, and form chains of cells filled with chlorophyll. When the antheridia are ripe, the cells of the apical, covering layer separate from one another, the internal mucilage, swarming with thousands of active, motile spermatozoa, is forced through the narrow canal at the apex of the antheridia which opens externally, and ap-

pears in drops of considerable size upon the upper surface of the antheridial disc. The spermatozoa, which are hardly half as large as those of Pellia, consist of a delicate thread, slightly thickened at one end, and drawn out into a thin long process at the other. I could perceive no trace of lateral cilia.*

I have only been able to examine the antheridia of *Rebouillia hemispherica* when fully developed. They are imbedded, as Bischoff's beautiful observations have shown,† in half-moon-shaped cushions, which appear superimposed upon the median line of vegetative shoots, usually upon those which bear a fruit-receptacle. As the outside of these cushions often bear rudimentary leaves, it appears to me probable that these cushions may be considered to be weakly developed shoots, resembling to some extent, in their development, the portions of the stem of Pellia which bear archegonia (Pl. XVI, fig. 17). The antheridia are proportionably large, surrounded by flask-shaped cavities. In the youngest which I have examined there was still to be seen the covering layer of tabular cells (Pl. XVI, fig. 17), which, at a later period, is entirely supplanted, so that a membranous sac alone encloses the cells which produce the spermatozoa. The mouth of the antheridial cavities is not often on the level, like that of *Marchantia polymorpha* (Pl. XVI, fig. 17). It more frequently protrudes to a considerable height, in the form of a thick, conical point, like the antheridial envelopes of Riccia. The tissue of the antheridial cushions consists of very large cells, with transparent fluid contents.

The history of our knowledge of the Marchanticæ is most fully treated in Bischoff's work, already so often cited, and in the fourth part of the 'Naturgeschichte Europaischer Lebermoose,' by Nees von Esenbeck. Except this volume, I know of no connected treatise on the development of the Marchantieæ since the almost contemporaneous appearance of Bischoff's and Mirbel's‡ large works.

* Compare Thuret, 'Ann. d. Sc.,' iii sér., tom. 3, pp. 13, 14.

† 'N. A. A. C. L.,' vol. xvii, pl. lxix, f. 4, 6, 7.

‡ "Recherches sur la *Marchantia polymorpha*," 'Mém. de l'Acad. des Sc. de l'Inst. de France,' vol. xiii.

Many of the most interesting specialities are to be found in Gottsche's two writings above referred to. The above investigations of Mirbel and Bischoff are so generally studied and known that it would be superfluous to give even a short summary of the valuable results obtained by them. Good representations of the fruit and perianth of *Marchantia polymorpha* are to be found in Micheli's 'Gen. Pl.,' p. 2, and in Dillenius's 'Hist. Musc.', pl. xxviii, figs. *m*, *n*, who also figures the germination of the gemmæ. Micheli considered the male and female plants as different species; the relation of the two was first noticed by Rupp ('Flora Jenensis,' ii, 276), then by Dillenius (l. c., p. 524), and with certainty by Linnæus (SP. PL. 1137). Our present more accurate knowledge of the Marchantieæ dates from the publication of Schmidel's observations ('Icones pl.,' ed. ii, p. 109 *M. polymorpha;* p. 120 *Fegatella conica;* p. 133 *Preissia commutata*). Schmidel isolated the antheridia, and pointed out their mode of attachment to the tissue supporting them; he gave an accurate figure of the structure of the receptacle, and described the spontaneous detachment of the fruit-stalk of *Fegatella conica* from the tissue of the mother-plant. Hedwig ('Theoria generationis,' ed. ii, 1798) distinguished the enveloping cellular layer of the antheridia (p. 176), and found that in the young fruit the young perianth did not reach to the height of the mouth of the archegonium (p. 177).

The object of Mirbel, in his remarkable work on *Marchantia polymorpha* ('Mém. Acad. des Sciences de l'Inst. de France,' xiii, 1835) was to investigate fully the history of the development of this plant in all its specialities. This object was only imperfectly attained. Mirbel observed the germination of the spores. He came, however, to the erroneous conclusion that the newly added cells were produced on the outside of the existing cells (l. c., p. 347). This error arose from the circumstance that in young multicellular germ-plants which are furnished with only one rootlet, the cell out of which the rootlet is formed is very similar in shape and size to the germinating spore, whilst the latter is still unicellular, but when it has already developed a rootlet. His view of

the origin of the quadrangular stomate upon the vegetative shoots is to some extent erroneous, for he assumed such origin to lie in the disintegration of one four-sided cell, surrounded by four epidermal cells, which (four-sided) cell is, in reality, the mother-cell of the cells which enclose the stomate, and which afterwards separate from one another. H. von Mohl commented upon this error in the 'Linnæa' (1838) and in his 'Vermischte Schriften,' p. 252. Mirbel's representation of the origin of the stomate surrounded by more than four cells is, on the other hand, quite natural (l. c., p. 356).

With regard to the receptacles of the gemmæ, Mirbel believed that, at the time of their appearance, the superficial cellular layer of the flat stem became detached from the underlying tissue, and separated into converging teeth, which soon constituted the margin of the receptacle. Mirbel has rightly apprehended the unicellular, earliest state of the gemmæ (l. c., p. 350); his notion of the contemporaneous metamorphosis of the contents of the unicellular gemmæ into a multicellular tissue filling the cell was confirmed by Nägeli in 1845 ('Zeitschrift f. wiss. Bot.,' ii, p. 150). Mirbel's investigations of the germination of the gemmæ of Marchantia are of especial interest. He showed that that surface of the gemmæ which happens to be in contact with the ground develops rootlets, whilst the other one forms the upper surface by development of stomata and air-cavities; but that, twenty-four hours after being sown, and when only a few rootlets have grown out of the under side, the upper and under surfaces of the future plant have already become permanently differentiated. When gemmæ, which had been sown for this short period, were reversed, rootlets grew from that side, which having been formerly the upper, had become the under surface, whilst those rootlets which had sprung from the quondam upper, then the under surface, continued to grow, and bending themselves downwards, penetrated the soil. During the further growth of the gemmæ, however, each of the elongating lateral halves effected a semi-revolution around its axis, so that the surface which had been formerly the upper one again became the upper

surface of the newly developed portions. In cases where obliquely incident light intersected the smaller diameter of the inverted gemmæ, the younger portions of the latter bent themselves simply backwards, so that the original upper side was again turned to the light, and only rested upon the soil by the one reflexed end.

The under side, which by inversion had become directed upwards, never developed stomata, not even at the points directly exposed to the light; on the other hand, when kept in the shade and sufficiently moist, it sent out roots in every direction, and as it advanced in age exhibited prominent ribs (l. c., p. 355). Mirbel thought that the cell-multiplication in the interior of the gemmæ, was an interpolation of new cells between those already present (l. c., p. 352). He has not discussed in detail the mode of ramification of the Marchantieæ, although the inquiry into this is closely connected with the investigations as to the mode of development of the gemmæ. Even at a still later period, up to the present time, this ramification has generally been described as dichotomous (as, for instance, by Nees v. Esenbeck, 'Naturgesch. Europ. Lebermoose' iv, (1838) p. 83), whereas, in point of fact, it represents a Dichasium. We are indebted to Mirbel for very accurate accounts of the structure of the developed fructification, especially of the relation of the longitudinal forks of the stem, which are traversed by the rootlets, to the pileate expansion which bears the reproductive organs (l. c., pp. 346, 376). Mirbel was least successful in his investigations of the structure and development of the organs of sexual reproduction; his figures are certainly beyond all comparison more elegant and satisfactory than those of Schmidel and Hedwig, but in the knowledge of the more important circumstances he is not really a step in advance of the observers just named (l. c., pp. 377—381). Mirbel's investigations of the development of the spores and elaters were of great scientific importance, the more so because, in conjunction with Mohl's contemporaneous works on the same subject, they gave an impetus to the more accurate investigation of the visible processes of cell-formation and cell-multiplication. Mirbel pointed out the division of the contents of the spore-mother-

cell into four masses, each of which becomes a spore, and also the origin of the elaters, out of a previously thin-coated elongated cell (l. c., pp. 371, 382). In a treatise more particularly devoted to systematic questions relative to the Marchantieæ, Bischoff ('Nova Acta A. C. L.,' xviii, 1835) has communicated some interesting results; he proved that the presence of male plants of *Lunularia vulgaris* is necessary for the development of the fruit (p. 925); he pointed to the simple nature of the structure of the first shoot of the germinating spore in comparison with that of the shoots of the fully developed plant (p. 953). He has repeatedly and emphatically dwelt upon this point, and has endeavoured to distinguish these first shoots (as a prothallus) from the later ones ('Handb. Bot. Term.,' ii, p. 733; 'Bot. Zeit.,' 1853, p. 113), starting manifestly from the supposition that the formation of a prothallus is peculiar to the order Muscineæ, and that it must, therefore, be proved to exist generally in all liverworts (see Bischoff's definition of the Muscineæ in 'N. A. A. C. L.,' xviii, p. 958). Both Gottsche and myself have proved that there is no essential difference between the first shoot of the germ-plant and the later shoots ('Botan. Zeit.,' 1858, Supp., p. 45).

This difference of opinion can give rise to no real controversy. The formation of a prothallus is a universal phenomenon in the embryonal life of plants. The development of the germinal vesicle of the phænogams into the embryo, of the germinal vesicle of the vascular cryptogams into the rudiment of the leafy plant, and of the germinal vesicle of the Muscineæ into the fruit all commence with a kind of cell-multiplication, which, at least during the first process of division, differs from the later stages of development. The first, at least, of the permanent cells thus formed does not enter into the composition of the mass of the organ which is to be constructed; very frequently it dies. The same law prevails in the germination of the spores of ferns and of the Muscineæ. In the leafless Jungermannieæ, the Ricciæ, and the Marchantieæ, however, the boundary between the prothallus and the developed plant is not, as Bischoff considers, to be looked for at the point where the second shoot is attached to the first, but at the point where

the primary, atypical divisions of the spore-cell terminate, and the regular arrangement of the cells of the first shoot commences. As far as present observations extend, this point is generally only a few cells distant from the hinder end of the germ plant.

Few works upon the Marchantieæ have appeared since those of Mirbel and Bischoff. Gottsche has given a very accurate account of the germination of *Preissia commutata* ('Nova Acta A. C. L.,' xx, p. 388); Grönland has published some observations upon the same subject, and upon the germination of *Marchantia polymorpha* and *Lunularia vulgaris* ('Ann. d. Sc. Nat.,' iv sér., vol. i, 1854, p. 22); and lastly, Henfrey has written upon the development of the spores and elaters of *Marchantia polymorpha* ('Trans. Linn. Soc.,' vol. xxi). The latter paper contains the important observation that the interior of the young capsule is filled with elongated, closely packed cells. A portion of these radiating cells consists of narrow, thin tubes, tapering at both ends; these are the young elaters; the wider cells are the primary mother-cells of the spores. These wider, elongated cells are divided by transverse septa into rows of cubical cells, the spore-mother-cells. Sometimes longitudinal division also takes place in some of the rows of cells thus formed (l. c., p. 107). The process is, therefore, very similar to that which I have described in *Frullania dilatata*. The development of the spores of *Marchantia polymorpha* affords very little opportunity for the study of the processes of cell-multiplication, on account of the sensitiveness of the membrane and of the contents of the mother-cells. It is quite conceivable that Henfrey might have failed to see nuclei during the examination of the cells in water or iodine (l. c., p. 109).

Motile spermatozoa were first observed in Marchantia by Unger ('N. A. A. C. L.,' xviii, p. 791, 1837). In his figures (l. c., pl. lvii, fig. 4) he represents correctly the relation of the two oscillating cilia of the fore end of the spermatozoon to the body of the latter, but without noticing that the duality of these cilia is normal. Meyer also ('Wiegman's Archiv,' 1838, i, p. 212) believed the spermatozoa of Marchantia to be furnished with only one long

"tail," an unfortunate expression, inasmuch as the filiform portions take the lead when the spermatozoon is in motion. Thuret's figures of the spermatozoa of the Marchantieæ are very accurate ('Ann. d. Sc. Nat.,' iii sér., xvi, pl. xii; Marchantia, Fegatella, and Targionia).

CHAPTER VI.

MOSSES.

THE stems of mosses grow by continually repeated divisions of the blunt, conical, apical cell. This cell is pointed beneath; the division takes place by means of septa inclined in different directions. All mosses are alike in this. The form of the terminal bud is very various; it is narrowly pointed in Sphagnum and *Racomitrium ericoides* (Pl. XXI, fig. 19); it is blunt in Phascum and in many others; hemispherical in Hypnum; and very slightly arched in Polytrichum and *Dicranum scoparium*, where it is, in fact, almost a level surface, upon which the youngest leaves are arranged concentrically.

The apical cell of the stem of Sphagnum is pointed beneath, where it has three surfaces; and this three-sided pyramid is deeply imbedded in the adjoining next older cells of the end of the stem. These cells were separated from the inner cavity of the terminal cell by the formation of septa traversing that cavity. Each new septum which is produced in the apical cell is parallel to one (and that one the oldest) of the lateral surfaces, and cuts the two others. The newly formed cell of the second degree has the form of a body with rhombic fore and hind surfaces and with four rectangular lateral surfaces, one of which, the smaller one (the free outer wall of the cell), is slightly arched. The successive septa produced in the apical cell are therefore arranged spirally, and the spiral is normally a left-handed one, in accordance with the arrangement of

the leaves.* Each cell of the second degree divides very soon after its separation from the apical cell, by a septum at right angles to the longitudinal axis of the stem, which septum cuts the free outer wall, and also that lateral wall of the cell which is turned towards the apical cell.

* The first correct account of the cell-multiplication in the outermost apex of the stem of Sphagnum was given by Nägeli ('Pflanzen. physiol-Untersuchungen,' i, Zurich, 1855, p. 76). I had previously ('Vergl. Untersuchungen,' p. 60) erroneously conceived the process to consist in the repeated division of a two-surfaced, pointed, apical cell, by means of septa alternately parallel to either of the two lateral surfaces. The origin of this error was as follows:—When the arched apex of a very slender paraboloidal cellular body consists of a single terminal cell (as is the case with the ends of the stem of Sphagnum and Equisetum), a portion of the lateral edges of the apical cell will usually be the only part clearly visible when the body is viewed from above. The edges of the neighbouring cells of the second degree will not be seen. These edges form arcs, the curvature of which is greater in proportion to the size of the cells of the second degree, *i. e.* in proportion to the size of that portion of the terminal cell which is cut off to form the cell of the second degree. If the edges of the apical surface of the terminal cell of the bud extend so deep down that at the spot where each two intersect the sides of the bud possess a high degree of inclination, then, when the body is viewed from above, the middle part only of each edge of the apical surface can be clearly seen.

When the apical cell has the form of a three-sided inverted pyramid, with its apical surface highly arched, and divides by septa arranged in a continuous spiral order, and parallel to one of the lateral surfaces, then one of the edges of the apical surface must, immediately after each division, be considerably shorter than the two others. This fact is more clearly perceptible in proportion to the size of that portion of the cell which goes to form the cell of the second degree. In a system of similar spherical triangles, with a common centre, constructed by drawing successively within each triangle arcs parallel to each one of its sides, it will be found that one of the three arcs of each successive triangle is considerably shorter than the other two, the difference being greater in proportion to the curvature of the arcs, and to their distance from the respective parallel sides of the next outer triangle (see the Diagram, Pl. XVII, fig. 5*b*). When the length of the arcs exceeds 90°; when the length of the transverse diameter of the outer surface of a cell of the second degree amounts to one half of the diameter of the cell of the first degree from the division of which it originates; and lastly, when at the moment of division (by virtue of the innate growing power of the plant) the form of the apical surface of the cell of the first degree is not that of an equilateral, but of an isosceles spherical triangle, then it may happen that the points of intersection of the two larger arcs with the third (very short) arc may fall quite outside the apical, vaulted surface of the organ, when the latter surface is viewed under the microscope directly from above. These remarks apply almost exactly to the apices of the stems of Sphagnum and Equisetum, if observed immediately after the occurrence of division in the apical cell. A figure of the upper surface of the terminal cell is then obtained, which is strikingly similar to the apical aspect of the two-surfaced segment of a spheroid (Pl. XXII, fig. 4). Now, since in other instances (as in the apices of the stems of liverworts, of Selaginella and of certain ferns, and in the organs of fructification of mosses &c.) I had frequently ascertained that the multiplication of the apical cell undoubtedly took place through division by means of

The cell of the second degree is thus divided into an upper daughter-cell, with three-sided fore and hind surfaces, and an under, four-sided cell (Pl. XVII, fig. 2). The free outer wall of the former forthwith becomes arched outwards, and is recognisable as the rudimentary cell of a leaf. The latter (the lower cell) divides by means of longitudinal septa, alternately tangential and radial to the axis of the stem, which division continues until the completion of the full number of the cells of the portion of the stem in question. There is no very great regularity in the succession of these divisions. Sometimes one, sometimes the other, occurs first; frequently one step of the ordinary succession is passed over, and made good at a later period. In every case, however, one phenomenon is constant—at a point near the end (of the stem), about three cells downwards from the apical cell, the number of the cells of the circumference of the young stem is eight. An inequality in the multiplication by radial longitudinal septa of the cells of the third degree also occurs regularly; one of these cells in each zone of the stem must lag about one division behind the two others. For if this multiplication in the cells of the third degree were uniformly active, it would follow that, inasmuch as *three* cells of the third degree must occur in each transverse section of the stem, the number of cells of each girdle of the outer surface of the stem must be a multiple of three.

A transverse section of the perfect stem usually exhibits a number of peripheral cells which is a multiple of eight.

septa inclined alternately in only two opposite directions, I was led to believe that I must necessarily assume the same to be the case in Sphagnum and Equisetum, where I observed the pointed apical cells of the stem-bud had the appearance of being two-surfaced. The cases of three-sided apical cells which came under my observation, and of which I have given figures in pl. xix, fig. 7, of the 'Vergleichende Untersuchungen,' I considered to be instances of a mode of growth which caused a change in the form of the apical cell between the period of each two divisions. Later observations have convinced me that Nägeli's representation of the mode of increase of the apical cell of the stem of Sphagnum, and Cramer's account of the similar process in Equisetum, are correct. From this error there necessarily arose, in the case of Sphagnum, an additional one, viz., in the account given of the further division of the cells of the second degree, and in the statement that the rudimentary cells of the leaves were derived from these latter cells, which error I have corrected in the text above.

In slender branches, especially those which hang downwards, the bark consists very regularly of only eight longitudinal rows of cells. In the younger parts of the bud the axile cells of the stem are more elongated longitudinally than the peripheral cells, a circumstance which has a remarkable influence upon the slender form of the end of the stem. The arrangement of the cells of the interior of the stem into triangular plates, inclined inwards to the axis of the stem, arises from the fact that all the cells of the third part of a transverse section of the stem are derived from a single cell of the third degree. Each of these plates is higher by a portion of the length of a cell than the adjoining plate on one side of it, and is exceeded by the same portion of the length of a cell by the similar plate on the other side of it. The difference of height of two such cellular plates is almost always less than half a cell, a circumstance from which it must be concluded that the elongation of the cells of the stem preponderates in their upper portions. The above-mentioned arrangement is most clearly seen in a perfectly axile longitudinal section of a Sphagnum bud, made at some distance from the apex; if the section deviates only slightly from the longitudinal axis of the bud, the arrangement is partially or entirely undistinguishable.

In all the cells of the periphery of the stem (with the exception of the cells of insertion of the leaves) a transverse division occurs a short time before, or contemporaneously with, the termination of the cell-multiplication of the end of the stem, in a radial direction (Pl. XVII, figs. 1, 7). This multiplication does not continue in the cells of the interior of the stem, which are elongated, instead, during its continuance, to about double their former length; by this means the short-celled bark is differentiated from the long-celled axile-tissue. The multiplication of the stem-cells in the diametral direction is caused by the division of the slightly elongated cells of the interior of the stem, by means of septa tangential to the axis of the stem, alternating with divisions by radial longitudinal septa. The number of these cells in the transverse diameter of the stem increases tenfold from the place of insertion of

the youngest (already multicellular) leaf, to the place where the stem ceases to increase in thickness (Pl. XVII, fig. 1). This cell-multiplication does not, however, occur exclusively in a specific group of cells, such as is found in many vascular plants somewhat in the form of a cylindrical envelope. It is no doubt true that the cells in which division especially occurs are those of a conical envelope lying underneath the outermost cellular layer of the conical mass of cellular tissue. But the cells of the inner layers are by no means passive (Pl. XVII, fig. 1). During these processes the cells of the outer surface divide by radial longitudinal septa, and the cells of more vigorous shoots also by tangential longitudinal septa, so that the above peripheral cellular layer becomes transformed into a double, triple, or quadruple layer of cells (Pl. XVII, fig. 1). In more slender shoots the latter form of cell-division is suppressed: the cells of the periphery of the stem certainly increase in number, by the formation of radial longitudinal septa, whilst they keep pace with the increase of the periphery of the axile cellular string; the bark, however, remains, for a time at least, a simple cellular layer (Pl. XVII, figs. 7, 9). The basal cells of the leaves, which are buried to a certain depth in the tissue of the stem, and which are easily recognisable by their peculiar tabular, flattened shape, present in their ends, which are turned inwards, certain indications from which it can be determined whether a multiplication of the peripheral cells of the bark of the stem has taken place or not (Pl. XVII, figs. 1, 7, 8, 9).

Whilst the growth in thickness of the stem is thus in course of completion, its longitudinal growth is at a stand-still. It commences with increased activity at the spot where the conical form of the end of the stem passes into the cylindrical form of the older portion. All the cells become extended to at least twelve times their former length, and during this elongation one more final process of cell-multiplication takes place in them. The cells of the interior of the axile string are often (although not with any regularity) divided by transverse septa (Pl. XVIII, fig. 8). The cells of the periphery of this string divide still oftener by radial and tangential longitudinal septa. They become

very narrow and elongated (Pl. XVII, figs. 8, 9). Lastly, the cells of the bark, in all tolerably vigorous shoots, divide once more by tangential longitudinal septa, and in all cases very frequently by transverse septa (Pl. XVII, fig. 8). The bark thus becomes a stratum, consisting of from two to four layers of cells. In slender shoots this duplication of the cellular layers of the bark does not take place; *transverse* divisions only occur in their cells, so that even the fully grown bark consists of only one layer of cells.

A considerable thickening takes place in the walls of the cells of the axile tissue of the ends of the stems of fully formed shoots, whose longitudinal growth remains dormant from the end of autumn until the following spring, and whose densely crowded lateral shoots form a capitate accumulation round the end of the stem. This thickening is observable in a transverse section, when made about ten cells underneath the terminal bud. The thickened cell-membranes exhibit delicate pits (Pl. XVII, figs. 9, 9 ^{b}), which bring to mind those of the Coniferæ, inasmuch as they are usually (not always) arranged in longitudinal rows.* There are not any lenticular air-cavities between the ends of two contiguous pits; the ends are divided from one another by a thin, apparently homogeneous, membrane. The pits, when seen from the surface, exhibit within their circumference a narrow oval, but this appearance is probably caused by an interference of the rays of light incident from beneath. During the final longitudinal growth of the stem, during the remarkable expansion of the axile tissue of the internodes (which expansion is rarely accompanied by a transverse division), the thickening of these cell-membranes for the most part disappears. In old stems the membranes of the middle cells become rather thin again, and less brittle than in the younger portions. It is now difficult to distinguish any traces of the pits, which at an earlier period were so distinct. They have now the form of short, oblique fissures. The above-mentioned peculiar thickening of the cell-membranes only extends a short distance into the axile

* Figures of these pitted cells, agreeing with those previously published by me, have also been given by 'Schimper, Mém. prés. p. div. savants,' xv, pl. iv, f. 4.

tissue of the thin, lateral shoots. No trace of it is to be found in the innovations* which are developed from the ends of older, thinner, lateral shoots, and which, growing rapidly in length and thickness, ultimately exactly resemble the principal shoots in their mode of vegetation. On the other hand, after the completion of the final longitudinal expansion, a different mode of thickening occurs regularly in the elongated cells of the axile tissue of these thinner shoots, and also in that of the thick, principal shoots and of the lateral shoots. After the completion of this thickening the cell-membranes appear thick and indistinctly stratified, their colour being yellowish-brown or greenish brown, and sometimes very intense. This thickening is most highly developed in the narrowest peripheral cells of the axile cylinder; it diminishes rapidly in the wider, median cells.

When, from the arching outwards of its free surface, the rudimentary leaf-cell is recognisable as the mother-cell of the leaf, it embraces rather more than a third part of the circumference of the stem (Pl. XVII, figs. 3, 4, 5). At this period it still lies on the immediate boundary of the apical cell of the tip of the stem (Pl. XVII, fig. 2). When viewed from above it is clearly seen that the tangent of its free outer margin is parallel to the tangent of the arc which is represented by that one of the lateral edges of the apical surface of the terminal cell of the tip of the stem which is turned towards the rudimentary leaf-cell (Pl. XVII, figs. 4, 5). If, now, the successive divisions of the terminal cell were such that each third wall were parallel to the third last one (as in the diagram, Pl. XVI, fig. 5^b), it would follow that, inasmuch as each cell of the second degree produces a leaf, the leaves must be arranged under one another on the stem, in three exactly parallel, longitudinal rows. Accurate examination, however, of a terminal bud shows that even in the youngest portions of the bud this is not so. Even here also the youngest leaf-rudiments have the arrangement which is characteristic of a later

* Schimper, l. c., pl. xvi, f. 1.

period, viz., that of a spiral, usually a left-handed one, with divergence represented by the fractions $\frac{2}{3}$, $\frac{3}{8}$, or $\frac{5}{13}$.* This circumstance can only be accounted for in two ways. It is possible that, contemporaneously with or immediately after, the formation of each leaf, a certain twisting of the portion of the stem beneath it might occur. This assumption, however, is negatived by observation. It is easily seen that even the two youngest leaves of the bud have always the same divergence as the older ones (Pl. XVII, figs. 3, 4, 5). The only other possible process is that the apical cell of the stem may change its form between each two divisions in such a manner that each cell of the second degree, which is cut off from it by the formation of a septum parallel to one of its lateral surfaces, is withdrawn from the next previously formed similar cell by so much of the circumference of the stem as is equal to the distance of each leaf from the next youngest leaf beneath it. Observation shows that both immediately before and immediately after each division, the apical surface of the terminal cell has the form of an isosceles triangle (Pl. XVII, figs. 4, 5). The change of form of the cell, therefore, must arise from the fact that its increase in size, after division, takes place more particularly in a direction perpendicular to the new wall formed by the division; the youngest edge of the apical surface, which immediately after division represented one of the legs of the isosceles triangle, becomes, until the next division, relatively the shortest side; it forms the base of the triangle, which, by the greater elongation of the two other sides, has become again isosceles, but which deviates to the extent of the angle of divergence of the phyllotaxis from its previous position. The conclusions necessarily to

* A. Braun ('Nova Acta, A. C. L.,' xv, p. 279) and Schimper (l. c., p. 28) agree in representing the phyllotaxis on the middle of the stem of Sphagnum as having $\frac{2}{5}$ divergence. I have previously spoken of $\frac{2}{5}$ as the normal arrangement ('Vergl. Unters.,' p. 61), and I find this confirmed by subsequent observations of the median shoots (Pl. XVIII, fig. 5) of vigorous innovations and of germ-plants. Doubtless the $\frac{2}{5}$ arrangement also often occurs, of which I myself have figured an example (Pl. XVII, fig. 4), but, however frequent, I find it much less common than the other. Nägeli also found the $\frac{3}{8}$ and $\frac{5}{13}$ arrangements more frequent than the $\frac{2}{5}$. ('Pflanzen-physiolog. Untersuchungen,' i, Zurich, 1855, p. 77.)

be drawn from the position of the youngest leaves, and their relation to the apical cell of the stem in Sphagnum, lead to the same results which I had previously arrived at from direct measurement of the sides and angles of the three-sided apical cells of the stems of ferns.* In Sphagnum the object is not fitted for direct measurement; the steep inclination of the arch of the apical surface renders the accurate determination of the length of its edges impracticable. It is worthy of mention, however, that in the apical cells of Sphagnum-stems, with $\frac{2}{5}$ phyllotaxis, the apical angle of the triangle is visibly much more acute than in stems with $\frac{3}{8}$ or $\frac{5}{13}$ phyllotaxis. Probably in Sphagnum, as in ferns, the change of form which the terminal cell undergoes between two divisions does not depend upon a capacity for change of form innate in the cell alone, but is caused by the definite expansion of the cells of the second degree adjoining the apical cell.

The youngest conditions of lateral shoots which have come under my observation have the form of hemispherical arched cells, which are situated on the outer surface of the terminal bud, at a distance of three or four cells in a straight line from the apical cell, near the left margin of the third or the fourth leaf, and above the middle line, in the first case of the sixth, in the second case of the seventh leaf † (Pl. XVIII, figs. 16, 17). When a longitudinal section of a principal shoot is made through the longitudinal axis of the median shoot, and through that of a young lateral branch, it is clearly seen that the place of attachment of the young lateral branch, together with the cortical cells which lie between it and the next lower cell, occupies a portion of the outer surface of the stem exactly as large as that occupied by the insertion-cell of a leaf together with the cells of the tissue of the stem which are produced from the same cell of the second degree as the insertion-cell; one of the oblique rows in which the elongated cells of the interior of the stem are arranged reaches up to the place of attachment of the branch (Pl. XVII, fig. 1; Pl. XVIII, figs.

* 'Abhandl. Kön. Sachs. Ges. d. Wiss.,' v, 642. I shall return to this subject hereafter in speaking of the development of ferns.

† Considering the leaf as viewed from the outside and from beneath.

16, 17).* This circumstance justifies the conclusion that at the commencement of the formation of a lateral branch a portion of the apical cell-cavity, which, under ordinary circumstances, becomes the primary cell of a leaf, is applied to the formation of the rudimentary cell of the branch. It is probable that the formation of the branch takes place earlier than that of the leaf which stands at the same elevation in the ascending line of the spiral of the phyllotaxis. Assuming this to be so, the process can hardly be viewed otherwise than as a separation from the four-sided terminal cell, of an irregularly shaped cell of the second degree with a three-sided apical surface; after which separation the apical cell divides by a septum which is parallel to one of the shorter sides of the apical surface, and is inserted in the angle formed by the oldest lateral wall of the apical cell with one of the lateral surfaces of the rudimentary cell of the branch. This latter division would restore the apical cell to its three-sided pyramidal form. The direct observation of this process can only be accidental. Indications, however, of such a state of circumstances clearly exist in the occasional occurrence of very slender apices (of stems), whose conical end extends far above the last leaf-rudiment which is visible in profile, so that in the optical section of the naked cone two superposed cells of the second degree can be distinguished on one or on both sides.†

Most lateral branches ramify soon after their formation. Schimper (l. c., p. 30), judging from the anatomical structure of the points of origin of perfect branches, concludes

* In the 'Vergleichende Untersuchungen,' p. 62, I made use of an expression which might lead to the belief that I considered the lateral branches as axile in their origin. This arose from my having only had in view the relation of the elementary cell of the lateral branch to the leaf below it. Schimper, at p. 30 of his work on Sphagnum, has rightly objected that the position of the rudimentary as well as of the perfect lateral branches is always at the side, near the margin of the leaf which stands at the same elevation. I consider Schimper, however, to be in error (l. c., p. 30) in supposing that certain oval (occasionally stalked) cells, which are interpolated between each two moderately distant leaves, and which are seated upon the outer surface of the stem, are to be looked upon as the rudimentary cells of lateral branches. These cells are nothing more than the young state of the bicellular hairs, with oval terminal cells, which occur not unfrequently upon the stem of *Sphagnum*, and which are figured by Schimper himself (pl. v, f. 2).

† Such terminal buds have often been figured, for instance, by myself in the 'Vergl. Unters.' (pl. xiii, f. 1), and by Schimper (l. c., pl. iii, f. 2, 7).

that the branch developes a number of lateral branches before the commencement of the formation of leaves; and he treats the scale-like appendages of the young branch-buds, which I considered to be leaves, as being the rudiments of lateral branches (Pl. XVII, fig. 6). Continued observations have not afforded me a single phenomenon confirmatory of this opinion of Schimper's. I have found, without exception, that the lateral branches develope indisputable leaves at a very early period, almost close to their place of insertion into the principal stem (Pl. XVII, fig. 1), and I have never seen a branch of the second order inserted on a primary branch underneath the place of origin of the first leaf. The points at which the axile cellular strings are separated from the branches, often appear to be enclosed within the bark of the fully developed principal shoot (l. c., pl. iv, fig. 4); but this appearance is caused by the comparatively late commencement of the growth of this bark in the direction of its thickness; the bark is closely attached to, and grows round, the base of the branches, and strips off their lowest leaves.

I found that the development of the stem and branches of *Orthotrichum affine* agrees in all essential particulars with that of Sphagnum.

The first division of the rudimentary leaf-cell, which protrudes slightly above the circumference of the terminal bud, takes place by means of a septum springing laterally from its longitudinal axis, and perpendicular to the surfaces of the leaf. This division is succeeded by that of the apical cell, which takes place by means of a septum inclined in the opposite direction, meeting the one previously formed at an angle of 90° (Pl. XVII, fig. 3). By the repeated division of the apical cell by means of alternately inclined septa, the leaf grows in length. During this time the form of the apical cell is that of a low, three-sided prism, and the form of the cells of the second degree is that of a procumbent parallelopiped.

Contemporaneously with or very shortly after the formation of a new cell of the second degree, the next older one divides by a transverse septum, which, like all those which take part in the formation of the leaf of Sphagnum, is per-

pendicular to the surface of the leaf. The edge formed by the contact of this latter septum with the upper side wall of the mother-cell coincides exactly with the line in which the membrane just produced in the apical cell cuts the boundary wall of the cells of the first and second degree. The septum in question forms a right angle with the side walls of the cell of the second degree; its direction is, therefore, exactly the same as that of the septum by which the apical cell was contemporaneously divided. The inner of the cells into which the second youngest cell of the second degree is divided has a rather long, rectangular, basal surface. Both the cells of the third degree, which are produced by the division of the cells of the second degree, are soon divided, by longitudinal septa parallel to the side walls, into equal parts, whose basal surfaces are almost exactly square (Pl. XVIII, fig. 1). A similar process takes place upon each further division of the apical cell of the leaf. All the cells of the edge of the leaf which lie in the course of the prolongation of the line of direction of the newly produced septum of the apical cell divide, almost contemporaneously, with the apical cell, by septa whose direction coincides with that of the above-mentioned line (Pl. XVIII, fig. 1*b*). The result of these processes is that in all species of Sphagnum the young leaf, with the exception of its margins, appears divided into regular squares. With the exception of its edge, which appears composed of somewhat elongated cells, the entire surface of the leaf consists of cells whose basal outline is square, and each four of which are in contact at their edges. It is only occasionally that in these divisions one cell is passed over, and then one cell of the interior of the leaf is twice as wide as its neighbours, and its basal surface has the form of a parallelogram (Pl. XVIII, fig. 1; see one of the cells of the fifth of the oblique rows to the left).*

It is self-evident that, by the repeated division of the cells, the lower, older portion of the leaf increases consider-

* From the above-mentioned processes by which the chess-board-like arrangement of the cells of the young leaf is produced, Nägeli concludes that the division of one cell has a manifest effect upon the neighbouring cell, and causes the division of the latter in the same direction ('Pflanzen-phys. Unters.,' i, p. 78). On the other hand, I find in these facts a new ground for the con-

ably in width. Reckoning from the youngest leaf backwards, the sixth leaf of a shoot embraces one half of the stem; the twelfth embraces from five eighths to six eighths. Inasmuch as, during the multiplication of the cells of the base of the leaf, the cells of the stem upon which they are seated are in an active state of multiplication in a tangential direction, it follows that the place of attachment of the leaf to the stem continues, relatively, of a considerable width, amounting to one third of the circumference of the stem. Every section made through that part of a principal shoot which lies nearly under the apex meets, not only the longitudinal line of each eighth leaf, but also lateral portions of five intermediate leaves; so that, in most cases, the points of insertion of two leaves are only separated by one cell of the cortical layer.

When the division of the apical cell of the leaf (which division takes place by means of septa diverging alternately from the median line) ceases, a multiplication of all its cells, excepting those of the margin, commences; this multiplication begins at the tip, and progresses rapidly from thence to the base. Each of the square cells divides into two rather unequal parts by means of a septum parallel to one of the sides, but not exactly traversing the middle point of the cell (Pl. XVIII, fig. 2, below, to the left). The larger of the two is then divided, by means of a septum parallel to the narrow sides, into two cells of unequal size, the larger being square and the other somewhat elongated (Pl. XVIII, fig. 2). After the termination of these divisions the surface of the leaf consists of a system of square cells, each of which is surrounded by four oblong cells.

In the oblong cells chlorophyll-granules are produced, which increase rapidly and considerably in number and in size (Pl. XVIII, figs. 3, 9). On the other hand, the pale-green, highly refractive, and finely granular mucilage, which

clusion which I had previously drawn from similar appearances ('Abhandl. Kön. Sachs. Ges. d. Wissensch.,' vol. iv, p. 161), viz., that the growing power which regulates the form of compound vegetable organs is mainly proportionate to the form and number of the new cells in process of production, and that such power does not exhibit itself in each peculiarity of the process of cell-multiplication.

fills the larger square cells, disappears, after having become turbid and grumous, but without dividing into bodies of any definite form. The contents of these latter cells become clear like water. A considerable expansion of the leaf-cells now ensues, especially in the longitudinal direction. It begins at the apex of the leaf, and proceeds from thence rapidly downwards. The cells of the margin, which divided once, and only partially, by means of septa at right angles to the edge of the leaf, cannot keep pace with the increase in size of the numerous median cells; the leaf assumes more and more the form of a cap. At the same time the first traces of the well-known annular and spiral threads begin to be visible upon the inner walls of the larger square cells. A longitudinal division of many (often of all) of the cells with watery contents frequently precedes the appearance of the threads, especially in *Sphagnum squarrosum*, so that each two thread-cells lie near one another (Pl. XXIII, fig. 4). Not unfrequently, also, many of the small chlorophyll-bearing-cells divide by transverse septa (Pl. XXVIII, fig. 3). In the mean time the chlorophyll-granules in the small cells, which form a complicated network between the thread-cells, increase considerably in size.

In the greater number of mosses, *e.g.* Phascum, Bryum, Hypnum, Polytrichum, whose early development has been admirably figured by Nägeli, the formation of the leaves agrees in the principal feature—that is to say, in the nature of the repeated division of the one apical cell—with Sphagnum. An essential difference exists, however, in the fact that the number of the cells in the leaves of these mosses increases considerably by the repeated bisection of the cells of the lower part of the leaf, even after the division of the apical cell has ceased, after the latter cell and its neighbours have expanded considerably, after the contents have become transparent, and the walls of the cells of the apex of the leaf have become considerably thickened. In Sphagnum this supplementary multiplication of the cells of the base of the leaf can never be distinguished. Upon the last division of the apical cell the lateral margin of the leaf consists of a number of cells (normally from eighteen to

twenty in *Sphagnum acutifolium*), which is afterwards only doubled by transverse division of the marginal cells. The above-mentioned phenomenon, on the other hand, is very distinctly marked in Polytrichum and Fissidens. It is well known that the leaves of the latter genus are arranged in two rows. The terminal bud is surrounded by the peculiar pocket-shaped duplication of the base of the last-formed leaf; each older leaf of the bud also encloses the younger leaves and the summit of the shoot in the already perfected duplication of its base. The very young leaves resemble the first rudiments of the leaves of Sphagnum. But when the leaf is only five cells in height, the method of cell-multiplication changes. As in Sphagnum, the cell of the second degree divides by a septum at right angles to the side walls. The septum which thereupon divides the outer of the newly formed cells into two, stands at right angles to the above septum, like the similar septum in Sphagnum; on the other hand, the membrane which originates in the inner cell is at right angles to the median line of the young leaf (Pl. XVIII, fig. 17, *a*). The two cells of the fourth degree belonging to the marginal cells of the leaf divide, at first, by a septum parallel to the margin of the leaf. The next septum, however, in both cells is at right angles to the margin of the leaf. The transverse division corresponding to this division is suppressed in the cells of the two rows adjoining the longitudinal axis of the leaf, in consequence of which these cells are double the length of the neighbouring cells (Pl. XVIII, fig. 17). The leaf continues to widen by the further division of the cells of its margin, caused by septa parallel to the edge. Sometimes individual marginal cells are divided also by longitudinal septa.

The formation of the *pocket* at the base of the leaf commences when the base of the leaf has attained a width of eight cells. At this time from five to eight of the lowest cells of that margin of the surface of the leaf which is turned towards the terminal bud become arched upwards to a considerable extent; the protruded portions are then separated from the primary cell-cavities by means of septa parallel to the surface of the leaf. By this means a raised line origi-

nates, which is attached laterally to the margin of the leaf, and consists of a longitudinal row of cells. These expand downwards from the longitudinal axis of the leaf, and exactly keep pace with the further multiplication of the cells from which they sprang. As the increase in width of the leaf is much less at the base than close above it, it follows that in the perfect leaf the commissure of the two parallel cellular surfaces appears to be considerably inclined sideways, running obliquely from the margin of the leaf to the base of the mid-rib. By the peculiar development of the bases of the leaves, nature has more than sufficiently compensated the youngest portions of Fissidens for the deficient protection which, owing to their mode of arrangement, the leaves would be able to afford.

When the young leaf of Fissidens has attained a length of $\frac{1}{8}'''$, the multiplication of the apical cell terminates. At this time the leaf retains the form which it had when in a younger state; it is less slender than when more fully grown. The further multiplication of its cells is produced exclusively by the continual division of those of its lower portion. The great activity of this multiplication is shown from the simple statement that the number of the cells of the proportionably small point of attachment of the leaf, when reckoned transversely, amounts to thirty.

The six longitudinal rows of cells adjoining the median line of the leaf of Fissidens become transformed into the mid-rib, by division produced by septa parallel to the surface of the leaf, and by the division of the newly formed cells by septa perpendicular to the surface of the leaf. The base of the mid-rib in the perfect leaf is immediately adjacent to the duplication of the lower part of the margin of the leaf.

The examination of half-developed leaves of mosses which are undergoing this process of cell-multiplication will afford one of the most convenient methods for the accurate investigation of the process of cell-division and the formation of chlorophyll. The object is not large enough for the microscopes of the present day. I believe, however, that I have already made out some interesting peculiarities in Fissidens. In the cells close to the base of the leaf the nucleus,

which has the appearance of a bright circle, is surrounded by an apparently homogeneous, pale greenish mucilage. The intensity of the green colour increases towards the apex. In cells which are about to divide, the formation of two nuclei, in the place of the primary one which has disappeared, precedes the formation of the transverse septum, as is the case generally in the higher plants; but, besides this, the green mucilage divides into two globular masses, each of which surrounds one of the newly formed nuclei (Pl. XVIII, fig. 18). Higher up, in cells whose multiplication has ended, the nucleus is no longer seen, but two large chlorophyll-bodies are found in the cell-cavity, in the interior of which bodies some starch-grains occur (Pl. XVIII, fig. 19). In the cells close to the apex of the leaf, whose walls have already become thick, the number of chlorophyll-bodies amounts to four, six, eight, or even more. The appearances which are seen during the formation of the chlorophyll-bodies in the leaves of Sphagnum and of *Phascum cuspidatum* are essentially the same as those observed in Fissidens. In leaves of Sphagnum where the division of the cells into three parts has extended as far as the base, and at whose apex the last active process (viz., the differentiation of the cells into those with, and those without, chlorophyll) has occurred, the cells of the base of the leaf are found to be quite filled with finely granular, yellowish green protoplasm, within which the nucleus appears in the form of a bright circle. Somewhat nearer to the apex of the leaf this protoplasm exhibits numbers of immeasurably small, dark-green particles, not individually distinguishable, by which the protoplasm is rendered turbid.

Hitherto all the cells of the leaf develope themselves equally. Towards the apex, however, the coloured matter within the quadrate cells diminishes more and more until it disappears altogether, whilst in the oblong cells it appears suddenly conglomerated into one or two spheroidal masses or chlorophyll-bodies. Nearer still to the apex of the leaf the chlorophyll-bodies in the oblong cells increase in number and diminish in size; this is manifestly caused by the division of the existing bodies, inasmuch as some of them may

occasionally be seen in the actual process of constriction (Pl. XVIII, fig. 4).

The perfect chlorophyll-bodies are small ellipsoids, somewhat flattened in the direction of the shorter axis, and having the substance of their periphery somewhat denser and more strongly coloured than that of their interior, so that they present a vesicular appearance. They usually contain one or more very small starch-granules.

In young leaves of *Phascum cuspidatum*, also, the less developed cells exhibit only one or two large chlorophyll-bodies; in more fully developed cells they become continually more numerous and smaller. The perfect bodies have a vesicular appearance, and usually contain several starch-granules; when the cell which surrounds them is ruptured, so that water is brought in contact with them, their entire mass swells up largely, running together ultimately into a shapeless jelly.

The previously described process of the formation of the large chlorophyll-bodies of Anthoceros is similar to that here mentioned. From these facts I drew the conclusion* that in young cells the chlorophyll is colourless, inasmuch as the colouring matter is dispersed throughout the mucilaginous cell-contents in the form of immeasurably small particles. As the development of the cell proceeds, the coloured portions unite to form globular drops, which are capable of multiplying themselves by division. This opinion was opposed to that of Nägeli ('Zeitschr. f. wissensch. Bot.,' H. 3 & 4, Zurich, 1846, 111), who assumes that the chlorophyll-bodies originate in the form of small, coloured granules, which gradually increase in size: it was, however, in accordance with Nägeli's view to the extent of assuming a vesicular structure in the chlorophyll-bodies, and it confirmed the fact, first pointed out by Nägeli, of the division of the latter bodies. The idea of a vesicular structure in the chlorophyll-bodies was opposed by H. v. Mohl, who relied upon certain appearances exhibited by those bodies when distended with water ('Bot. Zeit.,' 1855, 107, 109); but v. Mohl also, having eventually modified an earlier opinion, came to the conclusion that, however chlorophyll may

* 'Vergleichende Untersuchungen,' Lpz., 1851, p. 10.

be formed, nothing more seems necessary for its production than that green colouring matter should be formed in a cell, and should enter into combination with a mass of proteine substance. The investigations of Arthur Gris ('Ann. des Sc. Nat.,' iv ser., t. vii, p. 79), and of Sachs ('Sitzungsberichte Wiener Akademie,' xxxvii, (1859,) p. 108), have since shown that even in higher plants the chlorophyll-granules are formed by the disruption of a sharply-defined mass of protoplasm, often of no determinate shape, the green colour of which in certain cases becomes apparent *before* the disruption, in others *during* that process, and in others again *after* the disruption, and which mass of protoplasm is usually agglomerated round the nucleus.

The development of the leaves of mosses has lately been a matter of discussion. Nägeli asserted that the leaf grows exclusively at the apex and the edge. ('Zeitschr. für wiss., Bot.' ii, 175). Schleiden, on the other hand (Grundzüge, 3 Aufl), advanced a diametrically opposite opinion. According to him the leaf is pushed forwards by the multiplication of cells lying inside the circumference of the stem; the apex of the leaf being the oldest, and its base the youngest portion. With regard to the moss which Schleiden examined, viz., Sphagnum, this is absolutely incorrect; with regard to the leaves of liverworts and phœnogams it is only true in part, and to a very limited extent. Both observers have generalised too extensively from the results they have obtained in their investigations of mosses, although Nägeli subsequently limited his too vague conclusions, by acknowledging the frequent occurrence of intercalary cell-multiplication,* a very manifest fact long previously pointed out by Grisebach ('Wiegm. Arch.' 1846, p. 1). I have before attempted to show that, with regard to mosses, the truth lies between the two opinions. The first rudiment of the leaf is formed from an outwardly-protruding cell of the circumference of the terminal bud, by means of continually repeated division of the apical portion. In this rudiment

* Nägeli called this "*accidental cell-formation*," an expression the incorrectness of which he subsequently acknowledged, 'Pflanzen physiol. Unters.,' i, p. 83.

of the leaf, which in Polytrichum, for instance, attains a length of twenty-four cells, the apex is the youngest, the base the oldest portion. In most cases the cells of the base of the leaf-rudiment multiply actively, by which means the leaf acquires its ultimate number of cells. *Then* the cells of the base of the leaf are relatively younger than those of the apex.

The naked ends of those branches which are destined to bear fruit change the conical form of the vegetative bud into a flattened hemispherical one. Many of the cells of its upper surface grow out into short papillæ (Pl. XIX, fig. 1). Each of them divides by a septum inclined to the horizon; the upper one of the newly formed cells divides by a septum perpendicular to that already formed and inclined in an opposite direction. In the terminal cell of the cellular body, which makes its appearance above the surface of the bud, the division is continually repeated by septa inclined in different directions (Pl. XIX, fig. 1; Pl. XX, fig. 1). The cells of the second degree, except some of the lower, oldest (from two to six in number) cells, divide soon after their formation by radial vertical septa. Thus, in a short time, there is formed in the space surrounded by the youngest leaves, a number of short, cylindrical, cellular bodies, composed of four vertical rows of cells, intermixed, in many of the mosses, with long multi-cellular hairs, which have originated in the division by transverse septa of certain of the papillate superficial cells of the bud. These clavato-cylindrical masses of cells are the first rudiments of the archegonia as well as of the antheridia.

When the young archegonium has attained a height of from six to eight cells, all the cells belonging to one of the four perpendicular rows of cells of which (irrespective of the base and the growing apex) it consists, divide by septa parallel to the chord of the arc of the free, arched, outer wall, and cutting the side walls of the cell at an angle of about 45°, by which means the mother-cell is divided into an outer four-sided, and an inner three-sided cell. Each one of the newly-formed cells of the third degree (which form the continuation upwards of the string of diagonally-

divided cells) divides in the same manner immediately after its formation, such division being, in most instances exactly contemporaneous with the next division of the apical cell, very seldom somewhat later, often earlier (Pl. XX, figs. 2, 3).

The archegonium now consists of a central string of cells, which is surrounded by from four to six longitudinal rows of cells. There are far more frequently *six* rows, in consequence of the division of two of the original four, by radial longitudinal septa (Pl. XX, fig. 7). The archegonium resembles, therefore, in its development, as well as in its structure, the like organ in the liverworts. One of the cells of the central string swells to a remarkable extent, especially in width, whilst the upper end of the archegonium continues to grow. This cell, however, is never so near to the base of the archegonium, as in the liverworts; amongst the mosses which I have examined it lies lowest in Phascum and Archidium, where it is the third, fourth, or fifth, reckoned from below (Pl. XX, fig. 2; Pl. XXIII, fig. 13). Soon after it begins to swell the cells underneath it divide by transverse, and partly by longitudinal septa, whereby they expand only in length, not in breadth. This cell-multiplication is more active close under the swollen cell, than at the base of the archegonium. In Phascum those cells which surround the sides of the swollen cell divide, in the first instance, only by transverse septa and by longitudinal septa perpendicular to the outer surfaces (Pl. XX, fig. 4); the division of the above cells, by longitudinal septa, parallel to the axis of the organ, commences at a somewhat later period (Pl. XX, fig. 5). In other genera, as for instance, Funaria, Fissidens, Dicranum, and Polytrichum, the cells which cover the central cell of the ventral portion of the archegonium, are already divided by longitudinal septa parallel to the outer surface, long before the bursting of the apex of the archegonium; and this occurs particularly early in Sphagnum (Pl. XVIII, fig. 14), where, even before the opening of the top of the archegonium, this division is repeated in the inner as well as in the outer cells (Pl. XVIII, fig. 15). In this genus, consequently, the ventral portion of the archegonium is larger than in any other moss.

By these processes the lower portion of the archegonium becomes a pear-shaped cellular mass, which, at the point where it passes into the upper cylindrical portion (the neck) of the archegonium, surrounds the enlarged cell of the central string. In most instances the cell of the central string lying immediately above the enlarged cell, exhibits a considerable increase of its dimensions (Pl. XIX, fig. 5;. Pl. XX, fig. 4); this is especially remarkable in Sphagnum (Pl. XVIII, fig. 15).

Like all the cells of mosses the enlarged cell in question exhibits, from its first appearance, a manifest nucleus. In the very young archegonium the nucleus lies free in the middle of the cell, surrounded on all sides by protoplasm of uniform density (Pl. XVIII, fig. 14; Pl. XX, figs. 2, 4); at a later period, after the separation of the contents of the cell into two parts,—viz., the thick coating of the wall, and the less dense fluid contents of the median cavity,—the nucleus lies close to the side wall of the cell, surrounded by a thick accumulation of granular protoplasm, which sends forth radiate prolongations over the inner surface of the cell (Pl. XIX, figs. 5, 6). At this time there is seen underneath the primary nucleus of the cell, which is still very distinct, a small daughter-cell, occupying about an eighth part of the cell cavity, and having highly refractive contents, and a bright nucleus without nucleoli (Pl. XIX, figs. 5, 6). Contemporaneously with the appearance of this cell, the transverse septa, by which the separate cells of the axile longitudinal string of cells forming the neck of the archegonium are divided from one another, begin to dissolve. Even before these transverse septa have altogether disappeared, even before the dissolution of the transverse septa of the lowest of the cells of the axile string, and therefore before the formation of the canal which traverses the neck of the archegonium longitudinally, the central cell is found to be almost filled by a free spherical cell, which is either suspended freely, or touches the wall of the mother-cell on one side, and which contains a globular central nucleus (Pl. XVIII, fig. 15; Pl. XIX, figs. 7, 8, 20; Pl. XX, figs. 5, 6, 8). The primary nucleus of the cell is no longer present. These circumstances must lead to the conclusion, that the germinal

vesicle (*i. e.*, the small free daughter-cell of the central cell of the archegonium), grows with extraordinary rapidity, and displaces the dissolving primary nucleus of the central cell. In *Funaria hygrometrica* the ripe germinal vesicle is usually in close proximity to the transverse septum, which, even after the canal of the neck is fully formed, and sometimes even after the apex has opened, still shuts off the central cell of the archegonium (Pl. XIX, fig. 8). It often happens, however, in Funaria, in Phascum, and in Liverworts, that the germinal vesicle rests upon the bottom of the central cell (Pl. XIX, fig. 7; Pl. XX, fig. 9), or that it lies against one of the side-walls of the latter (Pl. XX, figs. 5, 6, 8).*

After the termination of the longitudinal growth, the cells of the apex of the archegonium divide by radial septa which are partly vertical and partly inclined sideways; and to some extent also by transverse septa. In many genera, such as Polytrichum and Sphagnum (Pl. XVIII, fig. 15), the new cells thus formed expand in a radiate manner, in consequence of which the apex of the archegonium appears strongly clavate. In the mean time, the walls of the string of cells which traverses the neck of the archegonium dissolve. The dissolution progresses from above downwards. Thus there originates in the axis of the neck a canal, containing only mucilaginous fluid, which leads to the large cell in the upper end of the ventral portion. Suddenly the cells of the apex separate from one another, and bend themselves backwards in the form of irregular flaps; in this state they form the so-called stigma (Pl. XX, figs. 6, 9, 13). The archegonium is now in the condition in which I consider it to be ready for impregnation. After the rupture of the apex of the archegonium, the mucilage which fills the canal of its neck not unfrequently oozes out of the opening, protruding above the funnel-shaped mouth in a hemisphe-

* The rapid disappearance of the primary nucleus of the central cell, and the agreement with it in size and form of the nucleus of the germinal vesicle, led me at first to the conclusion ('Vergl. Unters.,' p. 67) that the germinal vesicle might originate by free cell-formation round the primary nucleus of the central cell. The mode of its development, as given above, was first arrived at by me in 1854 ('Berichte Kön. Sachs. Ges. d. Wissensch. Math. Phys. Cl.,' 1854, p. 95).

rical form. Afterwards it is often agglomerated into globular masses,—some small and some large,—of transparent hyaline matter, as is the case in the Jungermanniæ. These processes may be seen especially clearly in *Archidium phascoides* (Pl. XXIII, figs. 1—3).

The product of the dissolution of the transverse septa of the string of cells which traverses the longitudinal axis of the neck of the archegonium frequently consists, in mosses, of a vermiform mass of highly refractive, hyaline, transparent mucilage (Pl. XIX, fig. 8). It seems that the formation of this string of mucilage is favoured by dryness of habitat. I seldom failed to find it in plants of *Funaria hygrometrica* which had grown in dry places. It is much less often found in plants taken from moist situations. In *Phascum cuspidatum*, a part of the contents of the wide axile string of cells lying immediately over the central cell of the archegonium very often assumes the form of an irregularly-shaped heap of coarse granules (Pl. XX, figs. 5, 8).

The first stages of development of the antheridia of mosses entirely correspond, as has been already stated, with those of the archegonia. A clavate mass of cellular tissue protrudes in a precisely similar manner above the upper surface of the end of the stem, consisting,—with the exception of the continually multiplying terminal cell and the cells of the base,—of four vertical rows of cells: in an almost precisely similar manner, a string of cells traversing the axis of the organ is formed by the division of the cells of one of the above rows; this occurs in the species of Phascum, Gymnostomum, Bryum, Eucalypta, and Funaria (Pl. XIX, figs. 1, 2, 3). In other cases diagonal septa originate in each of the four rows of cells, after which radial septa are formed in the outer ones of the new cells; by this means the antheridium becomes much more massive. This is the case in Polytrichum.

The inner cells of the young antheridium multiply very actively in all three directions (Pl. XIX, fig. 4). The cells of the upper surface divide only by septa perpendicular to the outer walls, and much less frequently than the inner cells. The antheridium thus becomes a clavate sac, consisting of a single layer of cells, which encloses an elongated

ellipsoid group of very small cellules adhering firmly to one another. In each of the latter, a spiral thread, consisting of nitrogenous matter which is coloured brown by iodine, is produced inside a lenticular vesicle which lies free in the interior (Pl. XX, fig. 16).

The tabular cells of the walls of the antheridium contain chlorophyll, and in the young state a flat lenticular nucleus also, whose major axis is parallel to the outer surface of the cell (Pl. XIX, fig. 4). When the antheridium approaches maturity, the colour of the chlorophyll-granules in many mosses becomes a yellowish-red. This is the case in *Funaria hygrometrica*, *Bryum cæspiticium*, *Polytrichum juniperinum*, *Gymnostomum pyriforme*, and *Neckera complanata*. The antheridia are usually intermixed with jointed hairs, the so-called paraphyses, whose terminal cells are often (as is the case in *Mnium hornum* and *Funaria hygrometrica*) swollen to a clavate form, and in Polytrichum produce a lancet-shaped expansion at the apex, originating from continual cell-division by means of differently inclined septa. The fully-ripe antheridium opens at the apex, and permits the escape of the small, enclosed cells, which contain the spermatozoa. The process is very easily seen in water on the stage of the microscope; and that the same thing takes place in nature, appears from the fact, that in every rich male inflorescence in mosses, empty antheridia, open at the apex, are found in company with ripening and ripe antheridia.

The bursting of the apex of the ripe antheridium of *Funaria hygrometrica* occurs thus:—the apical cell, and the youngest cell of the second degree, which is separated from the latter by a steep septum, exhibit a considerable enlargement of their outer wall, which expands in a vesicular manner; but the red colouring corpuscles of the cell contents, (whose interior is now usually occupied by a starch granule) do not enter into the expanded space. Careful investigation shows that the cuticle only of the cells of the apex of the antheridium is forced outwards,* and that the cavity between it and the firm membrane

* See Unger's figure of an antheridium of Polytrichum in the act of bursting 'N. A. A. C. L.,' v. xviii, p. II (1837), p. 790. Pl. 57, f. 1.

which immediately encloses the contents of the epidermal cells, is filled with a transparent, almost fluid, jelly, which can be nothing else than a product of the swelling up of the median layer of the walls of those cells which occupy the apex of the antheridium. Suddenly the cuticle of both the above-mentioned cells splits transversely; the contents of the antheridium are driven out between the detached cells of the epidermal layer in the form of a mucilaginous mass, shaped like intestines; these contents escape at first with great rapidity, and afterwards with a slower motion, which sometimes, by fits and starts, exhibits a momentary acceleration. The walls of the cellules in which the lenticular vesicles, which produce the spermatoza, are generated, are now swollen to a mucilaginous jelly. The latter is rapidly dissolved in water on the stage of the microscope, the vesicles are dispersed in the fluid, and are soon ruptured by the spermatozoa in their efforts to escape. The latter move about for some little time in the water, but with no very great rapidity. I have observed the motion to last for four hours in *Polytrichum formosum*. The mode of bursting of the antheridium leads to the conclusion that a radial expansion, and swelling up of the walls of the epidermal cells, especially of those of the apex, are at least as effective in producing the rupture, as is the outward pressure produced by the swelling of the contents.

The development of the antheridia of Sphagnum, which are situated singly in the axils of short lateral shoots, differs in some points of secondary importance from that which occurs in Phascum, Bryum, Funaria, &c. There is a long row of cells of the second degree in which division does not take place; a thin cylindrical double row of cells is produced, the end of which swells in a clavate manner. A few only (two or three) of the cells belonging to the double pairs of cells of the third degree which lie nearest to the apex of the organ, divide, by means of a septum parallel to the outer surface, into inner and outer cells (Pl. XVIII, fig. 11). The former become the mother-cells of the vesicles which produce the spermatozoa; they divide actively in all three directions until at last they form a spherical or oval group of closely-packed, small, tessellated

cells (Pl. XVIII, fig. 12), in each of which a spirally folded spermatozoon is produced in the interior of a lenticular vesicle. The cells which surround these central cells multiply by division, which takes place by means of septa perpendicular to the outer surface, and become the covering layer of the antheridium. On their outer side there is formed a glassy, transparent, very tough cuticle, which may be easily detached. When the organ is ripe the cuticle bursts at the apex; the vesicles enclosing the spermatozoa, having become free by the dissolution of the walls of their mother-cells escape at the opening, disperse themselves when under water in the surrounding fluid, and set the spermatozoa free, which then commence their revolving motion. Their spiral has from two and a half to three turns, and is sometimes a right-handed, sometimes a left-handed one. The anterior end of the spermatozoon carries two thin motile cilia attached laterally (Pl. XVIII, fig. 13). The covering cells* of the antheridia usually become isolated after maturity, like those of Anthoceros, Fossombronia, &c.; the cuticle holds together for a considerable time.

Schleiden was of opinion that the antheridium of Sphagnum was a large sac-like cell, in whose fluid contents the vesicles which produce the spermatozoa swam about freely. This notion is quite erroneous. Until just before maturity, the walls of the small, tessellated, closely-packed cells remain quite intact, each of them enclosing one of the vesicles. The nature of their arrangement is such, that the directions of the primary divisions of the seven-surfaced central cell of the very young antheridium may be easily recognised.

Fruit is developed only in those mosses where the archegonia are in the neighbourhood of antheridia. Any Botanist paying attention to the growth of mosses will be able to produce instances, in addition to those afforded by the older observers, to prove that female dicœcious mosses, in whose neighbourhood no male plants of the same species occur, produce perfect archegonia, but never fruit. At Leipzig, in

* The chlorophyll granules of these cells do not change colour when the antheridium is ripe.

certain localities, female plants only of *Mnium undulatum*, *Mnium punctatum*, and *Bryum cæspiticium* occur. In such places I have found every year numerous vigorous archegonia, but never a single fruit. When fruit is found in these species, male plants are invariably to be met with in the immediate neighbourhood.

I have not yet succeeded in finding spermotozoa in the central cell of the archegonia of Mosses near the germinal vesicle, as I have done in Ferns.* I have, however, seen in Funaria a moving spermatozoon which had penetrated through a third part of the length of the neck of an archegonium, which was ready for impregnation.

The first symptoms of the commencement of the development of a fruit, are a considerable enlargement of the germinal vesicle of the elongated ellipsoidal cell which fills the large cell in the upper end of the ventral portion of the archegonium (Pl. XIX, fig. 17; Pl. XX, fig. 10), and the appearance in it of a horizontal or slightly-inclined transverse septum (Pl. XIX, fig. 21; Pl. XX, fig. 10). In *Bryum argenteum* the upper part of the two cells divides again, once or twice, by means of septa parallel to that first formed (Pl. XIX, fig. 22$^{a, b}$). A septum inclined at a considerable angle, and seated upon the uppermost of these horizontal septa, is then produced. In Phascum, Funaria, and Fissidens, this inclined septum is formed immediately after the production of the first horizontal one (Pl. XX, figs. 11, 12). The upper terminal cell of the young fruit-rudiment is then divided by a septum inclined in a contrary direction to the one last formed, then by another parallel to the last but one, and so on. The longitudinal growth of the fruit-rudiment is carried on by division of the terminal cell by means of differently inclined septa (Pl. XIX, figs. 9—11, 22; Pl. XX, figs. 11—15).

The young rudiment of the fruit, when consisting of from one to four cells, may be easily detached (Pl. XX, figs. 11^{b}, 12$^{b, c}$). It occupies only a very small space of the upper half of the ventral portion of the archegonium, in the cavity of which it lies free (Pl. XX, figs. 11, 13). During its

* 'Ber. der K. Sachs. Ges. d. Wiss.,' 1854, p. 54.

further longitudinal growth, it presses together the neighbouring cells of the ventral portion, which have multiplied considerably during the development of the fruit-rudiment. This is very remarkable in Funaria (Pl. XIX, fig. 11). At the same time, the fruit-rudiment penetrates by its lower conical end continually deeper into the tissue of the archegonium.

The cells of the second degree which are formed by the continually-repeated division of the apical cell, and whose form is that of a flat semi-cylinder, divide by a radial vertical septum. This division usually takes place before the next division of the apical cell. The cells thus formed, each of which has a three-sided basal surface, divide by a septum parallel to the chord of the arc of the free outer surface, into an inner cell with a three-sided, and an outer one with a four-sided, basal surface (Pl. XIX, figs. 9, 10, 11, 11^b, 22, 22^b; Pl. XX, figs. 14, 15; Pl. XXI, fig. $2^{a, b, c}$; Pl. XXIII). The undermost margin of each such septum extends a little beyond the line of contact of the corresponding septum of the next lower cell. The next cell-division is that of the outer cells by a radial longitudinal septum. Then all the outer and inner cells of the group formed by the division of a cell of the second degree divide by horizontal septa, the inner ones often sooner than the outer ones (Pl. XIX, fig. 10). In the simplest moss-fruits, such as that of Phascum for instance, there ensues a repeated division of the cells of the circumference by means of horizontal septa, so that these latter cells appear only half as high as those of the centre (Pl. XXI, fig. 1, *a*). The cells of the periphery now divide by diagonal septa, the outer ones again by radial septa, and so on alternately, until the entire thickness of the fruit-rudiment is attained. At the same time division commences in the central cells of the middle and lower portions of the fruit-rudiment by means of septa parallel to the chord of the arc of the periphery, alternating with radial septa. This division leads to the formation of the string of elongated cells, which traverses the axis of the seta (Pl. XXI, fig. 1).

In mosses with more complex fruit, such as *Funaria hygrometrica*, and *Gymnostomum pyriforma*, the division

of the cells of the circumference by transverse septa first occurs after the production of an entire row of vertical septa, so that the string of elongated cells in the axis of the organ is far thicker. Even in vigorous specimens of Phascum, a division by a septum parallel to the chord of the arc of the outer surface precedes the formation of horizontal septa in the outer cells.

The above account of the division of the cells of the second degree does not apply in its entirety to the oldest of such cells. In the latter the above cell-multiplication proceeds only to a certain point; in the first two, three, or four of such cells, only the radial vertical septum is formed, and in the two three-sided cells thus produced, a tangential septum only; in the next the formation of radial vertical septa occurs in the four cells of the circumference, and the eight cells thus formed divide by septa cutting the last-mentioned septa at an angle of 90°. Thus the cell-multiplication progresses gradually upwards.

The thickness of the fruit-rudiment increases consequently from below upwards; it assumes the form of a spindle-shaped cellular mass. As long as the multiplication of its apical cell continues, the active increase of the cells in the direction of the thickness is always arrested for some considerable distance beneath the apex (Pl. XXI, fig. 3, 3^b).

In the mean time the cells of the ventral portion of the archegonium increase actively: so far as they encircle the fruit-rudiment this increase takes place only by division by means of septa perpendicular to the outer surface, but in the lower portion it is produced by septa turned in all three directions. The cells also of the hitherto flat end of the stem which bears the archegonia (both the impregnated and the unimpregnated),* expand and multiply actively, those in the middle more actively than those at the sides. By this means the end of the stem becomes conical; it bears at its apex the impregnated archegonium, and on its inclined surface the abortive archegonia and the paraphyses. This is

* In several species of Mnium, which exhibit a very large number of archegonia (as many as fifty) in one inflorescence, several archegonia are usually impregnated.

the origin of the Vaginula, the formation of which commences in Phascum and Bryum at a very early period, at the time when the fruit-rudiment only occupies the upper two-third parts of the archegonium (Pl. XX, fig. 15; Pl. XXI, fig. 4; Pl. XXIII, fig. 3). In Sphagnum the vigorous intercalary multiplication of the cells of the end of the stem which bears the archegonia begins at a much earlier period: even before the young archegonium has attained its full number of cells. The very short fructifying side-shoots of *Sphagnum cymbifolium* and *S. squarrosum* usually develope one, at the most two archegonia, with a remarkably fully developed ventral portion, and a strongly clavate apex. When the latter is about to burst the number of the cells of the end of the stem which bears the archegonia (and which in Sphagnum is conical) increases, without any change occurring in the circumference of the conical mass of tissue. Its upper surface bears rudimentary leaves destined to develope themselves in the following summer, at the commencement of the ripening of the fruit (Pl. XVIII, fig. 15).

By the continuous longitudinal growth of the fruit-rudiment its lower end is pressed continually deeper into the tissue of the lower part of the archegonium, until at last it reaches the parenchyma of the vaginula, to the base of which it penetrates. The pressure is caused by the resistance which the arcuate portion of the archegonium underneath its neck exerts upon the apex of the fruit-rudiment. The tissue of the stem itself resists the further penetration of the lower end of the fruit-rudiment. The ventral portion of the impregnated archegonium which has become the calyptra, now usually assumes the shape of a bell, in consequence, it would seem, solely of the expansion of its cells (Phascum, Pl. XXI, fig. 24, Gymnostonium, Eucalypta, Orthotrichum). The cells of its inner tissue become dissolved, only the single layer of the outer surface remaining (Pl. XXI, fig. 4). The hollow cavity between the latter, and the fusiform fruit-rudiment, is filled with watery fluid. The increased tension of the side walls of the calyptra, which is produced by the sudden and considerable expansion of the median cells of

the fruit-rudiment, causes the calyptra to break away by a circular fissure near its place of junction with the vaginula. The calyptra is carried upwards by the rapid elongation of the fruit-rudiment, upon whose apex it is placed.

At this period an active cell-multiplication commences (especially in the direction of the thickness) in the upper part of the fruit-rudiment, a little beneath the apex. The cells of the apex itself take no part in this new production (Pl. XXII, fig. 6). When the repeated division of the cells of the outer surface of the rudimentary fruit has increased the diameter of the part nearly under the apex by a certain number of cells (in *Phascum cuspidatum*, for instance, to sixteen, in *Gymnostomum pyriforme* to eighteen) an air-cavity in the shape of a hollow cylinder is formed nearly under the outer side of the slightly swollen upper end of the rudimentary fruit. This cavity divides the axile portion of the rudimentary capsule from the peripheral part, or capsule-wall. The latter in most species of Phascum has only three layers of cells (Pl. XXI, fig. 5); in *Phascum bryoides* and *Archidium phascoides*, it has only two (Pl. XXIII, figs. 5, 6, 8); in *Gymnostomum pyriforme* it exhibits in its lower portion five, in its upper, three layers of cells (Pl. XXII, fig. 7).

The primary mother-cells of the spores originate in an annular layer of cells of the axile portion of the rudimentary capsule. In Phascum and Eucalypta this layer is the second, in Gymnostomum and Funaria the third, reckoning inwards from the periphery of the central portion of the young capsule, which central portion is surrounded by the swollen, hollow, cylindrical air-cavity. The adjoining outer cells divide at a very early period by septa parallel to the axis of the fruit, and most of the inner ones of the newly-formed cells divide by horizontal septa (Pl. XXII, fig. 8). In consequence of this Phascum and Eucalypta have two, Gymnostomum and Funaria three layers of cells separating the hollow, cylindrical air-cavity from the layer of primary mother-cells (Pl. XXI, fig. 5; Pl. XXII, figs. 7, 10).

When the young capsule of *Phascum cuspidatum* is from $\frac{1}{4}'''$ to $\frac{2}{3}'''$ in length, the primary mother-cells (in which by often repeated cell-production the spores are formed) surround

the columella. The latter consists of a central group of smaller cells with thinner walls, and a peripheral layer of cells containing chlorophyll, which adjoins the mother-cells of the spores. The cells of the outermost of the two layers, which adjoin the primary mother-cells, are four times as large as those of the inner layer.

The cells of the layer of the columella adjoining the primary mother-cells, as well as those of the future inner wall of the capsule, are distinguished in a remarkable manner from all other cells of the *theca*, by the great concentration of the cell-contents, which are rich in dextrine. The large cells of the centre of the columella contain small amyloid masses of peculiar structure: minute firm granules, which become intensely blue under the action of iodine, are embedded in a gelatinous mass, which assumes a light blue colour under the same action.

The primary mother-cells, at this stage of their development, contain a large central nucleus, which has usually only one nucleolus, and somewhat transparent fluid contents (Pl. XXI, fig. 5; Pl. XXII, fig. 9). The remaining contents of the cell, which consist of a thick fluid mucilage rendered turbid by numerous granules, make it somewhat difficult to distinguish the outline of the nucleus.

The greater number of the primary mother-cells divide, as the fruit becomes developed, by means of a longitudinal or transverse septum perpendicular to the outer surface of the theca; more rarely by means of a longitudinal septum parallel to that outer surface (Pl. XXI, fig. 6). The disappearance of the primary nucleus of the cell, and the production of two new nuclei, precede the appearance of this septum. The contents divide into two halves, each of which surrounds one of the newly-formed nuclei (Pl. XXI, fig. 6, *b*); at the point of contact these two halves secrete the new cell-wall, which consists of a very delicate layer of cellulose (Pl. XXI, fig. 6, *a*).*

Sometimes when the development of the fruit is very active, the above division is repeated in the secondary

* The two halves represented in the figure have contracted under the influence of water, to which, in Phascum, they are very susceptible.

mother-cells. Usually, however, immediately after the formation of the secondary mother-cells, the tertiary mother-cells, *i. e.*, the spore-mother-cells, are produced.

Owing to the want of transparency of the cell-contents the nucleus of the secondary mother-cells can with difficulty be distinguished. It is, perhaps, impossible to make out what part it plays in the formation of the spore-mother-cells. A nucleus with a large nucleolus is very indistinctly seen through the grumous contents of the perfect tertiary mother-cell. The spore-mother-cells lie in twos, very rarely in fours (Pl. XX, fig. 7), quite free and detached in the inner cavity of the primary mother-cells. The second condition can easily be looked upon as the result of the suppression of the formation of the secondary mother-cells. A long series of comparative measurements has convinced me that the latter do not increase in size during or after the formation of the spore-mother-cells, and if this be so, the formation of the last-mentioned cells can only take place by the occurrence of a considerable contraction of the entire contents of the cell, either before or immediately after its division into two halves, upon the entire surface of which (two halves) cellulose is then secreted. I believe that I have actually seen such a process of transition (Pl. XXI, fig. 9).

The membrane of the mother-cells, primary, secondary, and tertiary, is coloured pale blue by iodine. When brought under water its substance swells rapidly, especially that of the inner younger layers. The membrane of the tertiary mother-cells swells the most, that of the primary ones the least. This peculiarity of the wall of the spore-mother-cell affords one of the most striking proofs of the independent nature of the primordial utricle. The spore-mother-cell, when placed in water on the stage of the microscope, rapidly swells to double its original size, its wall being excessively distended. The cell contents, which are plainly surrounded by a thin layer of soft matter very like a delicate membrane, swell slightly or not at all; they (the cell-contents) lie free in the inner cavity of the cell in the form of a closed vesicle, surrounded by watery fluid. Individual points of the primordial utricle

sometimes exhibit slow expansions and contractions similar to those of many of the inferior animals; for instance, the smaller Amœbæ. It is especially in such cases that the delicate mucilaginous membrane which encloses the cell-contents may be most clearly observed.

By continued absorption of water the primordial utricle becomes pressed laterally against the cell-wall; the granules which float in its fluid contents exhibit active molecular motion. Ultimately, the cell-membrane is ruptured, usually at the spot where the primordial utricle is in contact with it, and the latter escapes through the fissure. It then usually bursts, but occasionally I have seen the primordial utricle glide out through the fissure of the cell in the form of a closed, tightly stretched globular vesicle (Pl. XXI, fig. 8). The internal granules (consisting of starch and a substance rendered brown by iodine), continued their active molecular motion, which stopped suddenly, when a drop of diluted watery tincture of iodine was applied. The membrane of the primordial utricle shrivelled up to some extent, and assumed a yellowish-brown colour (Pl. XXI, fig. 8, *b*).

In one instance I observed a very peculiar state of the primordial utricle. As I brought the object under the microscope, it floated freely in the form of a globular vesicle in the interior of the swollen cell. Afterwards it approached the cell-wall, and attached itself to one of the sides, assuming the form of a slightly compressed sac (Pl. XXII, fig. 1.) Half the cell-cavity remained empty, or at least contained only water. The primordial utricle gliding up to the inner wall of the cell commenced a slow rotatory motion.

It has been already mentioned that the walls of the secondary mother-cells swell rapidly until they burst. If a section of a capsule containing fully formed tertiary mother-cells enclosed within secondary mother-cells is placed under water, it often happens that all the spore-mother-cells escape out of the ruptured secondary mother-cells, and become dispersed in the water upon the slide. At this stage of development of the capsule the fluid contents even of the cells of the outer capsule-wall attract

water powerfully. If a thin section of these cells is placed in water, very active currents may be observed over these cells, and in their interior.

In *Gymnostomum ovatum* the affinity of the substance of the walls of the tertiary spore-mother-cells for water is even stronger than in *Phascum cuspidatum*. If these cells are placed in water, the substance of the cell-membrane is almost immediately distributed through the fluid, so that the cell-contents remain behind, a shapeless, dissolving, round mass. In order to get a sight of these thick cell-membranes, it is necessary to observe the cells with the greatest promptitude immediately after they have been prepared for the microscope. On rare occasions the outermost lamella of these membranes holds together for a somewhat longer period in the form of a sac open at one end, after the rupture, by pressure, of the more highly swollen inner layers.

The contents of the mother-cell of the spores of Phascum divide into four portions, which after some time become clothed with a stiff membrane, and shrivel up under the action of alcohol. The first indication of this division is the appearance of a transparent line in the turbid cell-contents, passing transversely through the cell (Pl. XXII, fig. 2), or of two such lines cutting one another at right angles (Pl. XXII, fig. 3). The contraction of the contents manifestly occurs for the first time after their division into halves. The opacity of the cell-contents entirely prevents the observation of the behaviour of the nucleus of the spore-mother-cell during the formation of the spores.

The young spores lie in fours quite free in the mother-cell (Pl. XXII, fig. 4). Each spore exhibits a central nucleus, with a manifest nucleolus (Pl. XXII, fig. 5). The cell-contents consist of proteine combinations, dextrine, and starch-granules. Afterwards, when the formation of the exosporium commences, (at which period the absorption of the spore-mother-cells begins), oil-drops are visible in the interior of the spore, which, as the spore becomes mature, increase in number and size. During the time that the spores lie free between the inner wall and the columella, the cells of the innermost cellular layer of the former, and

of the outermost layer of the latter, abound with a saturated solution of dextrine, in which the nucleus floats in the form of a very sharply defined vesicle with less highly refractive contents.

During the secretion of the exosporium, the walls of those cells which are adjacent to the columella towards the apex of the fruit assume a deep-brown colour. It is in these cells that the partial disruption of the theca commences, by means of which the spores, which in the mean time have fully ripened, become free.

In *Gymnostomum pyriforme*, the multiplication of the cells of the upper part of the spindle-shaped rudiment of the fruit extends downwards far beyond the base of the future fruit. In this way an apophysis originates, which in the earliest stages of development far exceeds the fruit in size. After the separation of two annular layers of cells beneath the apex of the rudimentary fruit, by which means the vacant space between the outer and inner wall of the theca is formed, individual cells of the inner side of the outer wall grow so as to form chains of cells, the uppermost of which remain in connexion with the upper surface of the inner wall (Pl. XXII, fig. 7).

In the very young capsule of *Gymnostomum pyriforme*, at the time of the division of the cells which adjoin the outer and inner sides of the primary mother-cells, the latter have the form of very flat plates parallel to the axis of the fruit (Pl. XXII, fig. 8). During the further development of the theca, the transverse diameter of these cells increases considerably. A proportionably large nucleus with a large nucleolus becomes visible, floating freely in the fluid contents (Pl. XXII, figs. 9, 10). The length of the cell soon considerably exceeds its height and width.

At this time two new globular nuclei appear in the place of the vanishing primary nucleus (Pl. XXII, fig. 11). Half of the granular mucilaginous cell-contents accumulates round each of them; two globular masses of protoplasm are formed, which, after secreting cellulose over their entire surface, constitute the free spherical mother-cells of the spores (Pl. XXII, fig. 12).

If the primary mother-cells are unusually long or wide, they divide, according to the ordinary method of cell-multiplication, before the formation of the spore-mother-cells. Two of such primary mother-cells then adjoin *one* of the cells of the neighbouring cellular layers (Pl. XXII, fig. 12). In rare instances, four spore-mother-cells are found in one primary mother-cell (Pl. XXII, fig. 12^b).

The walls of the primary mother-cells, which at an early period are very sensitive to the action of water, become more so after the formation of the spore-mother-cells. If a longitudinal section of a fruit in this stage of development be placed in water upon a slide, the walls of the primary mother-cells immediately burst, and the spore-mother-cells are dispersed over the field of view. It is necessary to examine the preparations in some saline solution. A solution of carbonate of ammonia is the most useful.

In the natural course of things, the dissolution of the walls of the primary mother-cells follows soon after the formation of the spore-mother-cells. The spherical spore-mother-cells then lie free between the columella and the inner wall of the theca. Numerous mucilaginous granules surround the central nucleus, the substance of which is as clear as water (Pl. XXII, fig. 13).

During the further development of the fruit, the nucleus of the spore-mother-cell approaches the cell-wall, and usually assumes a lenticular shape. The granules of the fluid contents of the cell accumulate at its middle point, so as to form a spherical group (Pl. XXII, f. 14), in which the nucleus is sometimes partially embedded. This accumulation of granules divides afterwards into two halves (Pl. XXII, fig. 15); a spherical nucleus may often be seen in each of these granular masses (Pl. XXII, fig. 16). Each of the elongated groups of mucilage and granules divides anew into two parts; and then four spherical accumulations of coarsely granular protoplasm are found in the mother-cell. They are usually arranged at the four corners of a tetrahedron (Pl. XXII, figs. 17, 18), and very seldom lie in the same plane (Pl. XXII, fig. 19). Each of them contains a nucleus. The outline of the primary nucleus of the mother-cell becomes less and less distinct during

these processes, and at last that nucleus disappears altogether.

A spore is formed round each of the four secondary nuclei. The four spores do not nearly fill the mother-cell. A viscid fluid jelly fills the space between them (Pl. XXII, figs. 20, 21).

A layer of similar jelly is previously visible, forming the innermost layer of the membrane of the mother-cell; a bright space is formed between the firm lamella of the membrane and the boundary of the cell-contents (Pl. XXII, figs. 17, 19).

The first stages of development of the spore-mother-cell of *Funaria hygrometrica* resemble those of *Gymnostomum pyriforme*. Two secondary nuclei are formed outside the primary nucleus of the cell in the middle of an accumulation of granular mucilage (Pl. XIX, fig. 12). Afterwards four nuclei appear in the place of the two (Pl. XIX, fig. 14). The primary nucleus, which has become paler, now disappears. Suddenly the mother-cell divides into four parts of the form of a tetrahedron with a convex basal surface. This division is produced by six septa passing through each two of the four secondary nuclei. These four divisions constitute the special mother-cells, which in this genus have firm rigid walls, which at first are very thin (Pl. XIX, fig. 15). After the walls of these special-mother-cells have become considerably thickened by the deposition of gelatinous layers, a spore is produced in each of them, which, at its first appearance, entirely fills the mother-cell (Pl. XIX, fig. 16).

The formation of the spores of Funaria more nearly resembles that of the pollen of phænogamous plants, than the spore-development of Phascum, the similar process in Eucalypta, and that in *Gymnostomum pyriforme*. The material differences in the process of development of the spore-mother-cells in plants which are in other respects so closely allied, may, without hesitation, be considered as an indication of the fact, that the greater or less degree of firmness of the walls of the special mother-cells is an unimportant circumstance. The essential phenomenon in the formation of four spores or pollen-cells in the

interior of a mother-cell, is the contraction of the contents of the mother-cell (which contraction usually follows the division into two parts, or the repeated division into two parts of such contents), and the formation round the contracted mass or its divided portions of a new membrane, not attached to the inner surface of the membrane of the mother-cell. In plants, where the contents of the mother-cells divide into several portions before the contraction, the question whether special mother-cells with firm rigid walls are developed or not, depends simply upon the greater or less firmness of the substance which must be secreted by the cell-contents in order that the latter may be able to contract into a smaller space. This substance is always gelatinous, and usually tolerably firm. The thin, fluid nature of the jelly in *Gymnostomum pyriforme* forms a gradual transition to the state of circumstances found in Phascum, where the fluid substance which is found between the inner wall of the mother-cell and the contracted portions of the contents, behaves under iodine just like pure water. The latter cases seem to show that the contraction of the cell-contents depends upon an innate vital action, and not upon a mechanical compression (accompanied by the withdrawal of water), caused by the distension of the innermost lamella of the membrane of the mother-cell.

A great uniformity prevails in the process of development of the fruit of mosses so far as regards the most prominent features, viz., the cell-multiplication of the young fruit-rudiment, the separation of the sporiferous cellular layer from the remaining tissue of the theca, and the separation of the outer wall of the capsule from the inner one. The deviations from this process exhibited in *Archidium phascoides*, the ripe fruit of which is itself remarkable, are, therefore, the more surprising. These deviations are reducible to two:—1. Spores are developed by one cell only of the hollow cylindrical layer whose cells in other mosses become, one and all, primary mother-cells:—2. This cell and the daughter-cells produced by the division of its contents, gradually displace the whole of the inner tissue of the capsule. The peculiarities of

Archidium are, therefore, not altogether a departure from the typical development of moss-fruit, but are rather, with regard to the first point, a diminution, and with regard to the second, an increase, of the growing power usual in the allied forms.*

The antheridia do not differ essentially from those of the species of Phascum. The spermatozoa are rather large; they exhibit, very clearly, the two cilia shown by Thuret, to exist in the mosses generally. The structure of the unimpregnated archegonia is distinguished from that in Phascum only by the slight extent of the longitudinal development of the lower part (Pl. XXIII, fig. 1). I cannot confirm P. W. Schimper's statement as to the pleurocarpus fructification of Archidium. I find rather that the position of the archegonia and fruit exactly agrees with that which obtains in Phascum. The germinal vesicle is usually attached to one of the side walls of the central cell of the archegonium (Pl. XXIII, fig. 1). After impregnation the germinal vesicle enlarges to a remarkable extent, considerably expanding the ventral cavity of the archegonium, and pressing together the adjoining cells (Pl. XXIII, fig. 2). The cell-succession of the fruit-rudiment is that which is common to all mosses, depending upon the repeated division of the apical cell, by septa inclined alternately in two different directions (Pl. XXIII, fig. 3). The upper half of the fruit-rudiment soon increases in thickness, and ruptures the calyptra on one side, displacing it laterally (Pl. XXIII, fig. 4).

In the interior of the fruit-rudiment, underneath the second cellular layer (reckoning from the outside inwards), layers of cells parallel to the outer surface become disconnected: an intercellular space is formed, having the shape of an ellipsoidal covering, truncate at either end (Pl. XXIII,

* Schimper attempted to explain the nature of the ripe fruit of Archidium (Pl. xxiii, f. 11) by supposing that the whole of the interior of the fruit-rudiment became converted into mother-cells, and that only one spore was formed in each of them ('Rech. sur les Mousses,' Strassburg, 1848, Bryol. Europ. 1st ed., p. 2). In the 'Vergl. Untersuchungen,' I have objected to the above view, on the ground that imperfectly ripe spores exhibit a junction in fours. The observations given above (which were first published in the 'Reports of the Royal Academy of Saxony,' 1854, p. 102) were made upon living plants, kindly furnished by Messrs. Schultz, Bitsch, Tulasne, and Durien.

figs. 5, 6, 7). This is exactly the process which in all mosses causes the separation of the outer capsule-wall from the inner portion.

One of the cells of the interior of the capsule grows to a considerable extent, pressing the adjoining cells together. Its walls become thickened, and its contents rich in granular mucilage (Pl. XXIII, fig. 5). This cell is the sole primary mother-cell of the spores. Its primary position is always excentrical, separated by two layers of cells from the hollow cavity which adjoins the inner surface of the outer capsule-wall. Its vigorous power of growth continues whilst the surrounding tissue becomes disintegrated and dissolved. It now lies quite free in the cavity of the capsule, and falls out of the opened capsule without assistance. Four freely-floating mother-cells of the second degree are produced in its interior (Pl. XXIII, fig. 7), each of which divides into four special mother-cells (Pl. XXIII, fig. 8). Each of the latter produces one spore, so that the whole number of spores is sixteen. I have met with no exception to this in my numerous investigations.

The diameter of the newly-formed spore measures only one-sixth that of the ripe one. A delicate exosporium is distinguishable even in the earliest stages of development (Pl. XXIII, fig. 9). Afterwards it increases considerably in thickness, even before the entire dissolution of the mother-cells and the special mother-cells.

The inner capsule wall, and the inner cellular layer of the outer wall, are present for some time after the formation of the spores. These masses of cells are displaced, as far as the outermost cellular layer of the (now spherical) capsule, by the gradual growth of the spores. The membrane of the primary mother-cell remains to the last, enclosing all the spores. It is the membrane spoken of in the 'Bryologia Europæa' as the delicate spore-sac.

Few processes in the vegetable kingdom are so thoroughly understood as the germination of the spores of mosses, the production of leafy axes from individual cells of the confervoid pro-embryo. The admirable observations of Schimper* have entirely solved the last remaining

* 'Recherches sur les Mousses,' Strasburg, 1848.

difficulty. The investigations of Hedwig and his successors can be so easily repeated in many species, as, for instance, *Funaria hygrometrica* and *Barbula muralis*, that it would be waste of time to give a description of the phenomena. I will mention only some peculiarities which are not so well known.

The threads of the pro-embryo, whether they arise from the development of a spore, or from a cell of the surface of the stem or of a leaf*, exhibit in many species two very different modifications of development. The principal ramifications of the confervoid rows of cells are filled with assimilated matter, and contain very numerous chlorophyll bodies; their longitudinal growth, which results from repeated transverse divisions of the terminal cell, is unlimited. The lateral ramifications of these principal branches of the pro-embryo have only a limited growth; the terminal cells, when they cease to divide, assume a conical form. Moreover the lateral branchlets ramify in a complicated manner. Their contents are far less concentrated, their transverse diameter narrower, their chlorophyll more inclined to a yellowish tinge than is the case with the principal branches. These latter only are capable of producing true germs or leafy axes. The principal branches of the pro-embryo may, perhaps, be compared to stems; the lateral branches with limited growth to leaves. These phenomena are very remarkable in the pro-embryo of *Racomitrium ericoides*. Here, owing to their peculiar habit, the lateral shoots of

* I wish to add a few words as to the meaning of the expression "pro-embryo." By the word "embryo," is meant the bud capable of developing leaves and roots. Thus, we speak of the embryo of the onion, the potato, the hop. Now, when we find in the vegetable kingdom organs which differ from, and are of an essentially simpler structure than the leafy stem-rudiments which afterwards spring from them, but which must normally and necessarily in the course of their development produce embryos, I consider that I am justified in calling these organs "pro-embryos." Thus, I designate as a pro-embyro the proto-nema of a moss, whether it owes its origin to the germination of a spore or to the independent development of an individual cell of the leaf-bearing plant. I treat in the same manner the suspensor of Selaginella, of the Coniferæ, and of the phanerogamia. On the other hand, I do not designate as a pro-embryo the body which is produced directly from the germination of the spores of ferns, Equisetaceæ, Rhizocarpeæ, and Lycopodiaceæ, and which bears antheridia and archegonia, usually only the latter. This organ I call a "prothallium."

the principal branches, bring to mind most forcibly the leaves of *Trichocolea tomentella*. The pro-embryo of *Phascum serratum* is also remarkable, especially when it originates from the lower leaf-axils of developed plants. It is a fact, noticed especially by Nägeli, that the shoots of the pro-embryo are often subterraneous for a considerable distance; the transverse septa of such subterranean threads of the pro-embryo are not perpendicular to their cylindrical outer surface, but strongly inclined to it. The pro-embryonal threads of *Schistostega osmundacea* creep about for a considerable distance in the damp sand upon which this delicate moss is accustomed to vegetate. These subterranean rows of cells have such a narrow cavity, and their fluid contents are so transparent, and so deficient in granular matter, that they may be mistaken for some of the most delicate microscopical forms of moulds. When the terminal cell of such a thread is exposed to daylight, it immediately swells to a spherical form, and some beautiful emerald green chlorophyll-bodies are formed in its fluid contents. It would seem that a single chlorophyll-body is first formed, which is then increased by self-division (Pl. XVIII, fig. 16). The multiplication of the cells of the subterranean green portion of the pro-embryo, takes place by the continual division of its cells by means of transverse septa. The process is somewhat peculiar. The new septum does not pass through the mother-cell transversely, but the division commences by the protrusion, from the apex, of a small swelling which is at first hemispherical. The upper part of this protuberance increases rapidly in circumference, and becomes spherical; the lower part, on the other hand,—viz., the place of junction of the protuberance with the mother-cell,—widens to a very small extent, or not at all. Finally, when the size of the protuberance has nearly reached that of the mother-cell, a transverse septum is produced at the point of constriction, which cuts off the protuberance from the mother-cell (Pl. XVIII, fig. 16). Some time before the appearance of this septum, the first chlorophyll-vesicles are perceived within the protuberance. Usually only one such vesicle is at first visible, and the first symp-

* 'Zeitschrift für Wiss. Bot.,' Hft. 2, s. 172.

toms of it appear to be the production of colouring matter within a spherical drop of semi-fluid mucilage. It is certain that no chlorophyll-vesicles pass from the original cell-cavity into the enlarging protuberance. The single chlorophyll-vesicle often attains a very considerable size: in other cases four or more chlorophyll-vesicles are found in the protuberance before the formation of the septum which divides it from the original cell-cavity. Probably these have been produced by the repeated division of the original individual chlorophyll-vesicle. The number of chlorophyll-vesicles in the recently-formed cells of the pro-embryo is very frequently *four*. Older cells usually exhibit a larger number. It is but rarely that the chlorophyll-vesicles are agglomerated in the middle of the cell: when this is the case, the condition appears to me to be a diseased one.

The well-known metallic lustre which marks the spots overgrown by Schistostega is not caused by the chlorophyll-vesicles, but is fully accounted for by the spherical form of the individual cells. Dewdrops upon spiders' webs produce a precisely similar optical appearance.

I could not discover any nuclei in the dividing pro-embryonal cells of Schistostega. My observations having been made whilst travelling, I had not any tincture of iodine at hand.

Some of the older observers entertained curious opinions as to the influence of the moniliform rows of cells of the pro-embryo upon the development of the young plants. The most peculiar notion is that of Hübener, who says, "These bodies afford, by reflexion, the light which is necessary for the life of Schistostega; and in this way, as Eschweiler has very correctly remarked, they represent the moons of the vegetable kingdom." The glimmer of the protonema of Schistostega cannot be explained by phosphorescence. The plant never shines in the dark, even although previously exposed to a rather intense light, such as that reflected from a white cloud. The direct action of sun-light almost immediately destroys the vitality of the cells. This unusual sensitiveness to the rays of the sun is common to a number of other mosses also; for instance, *Calypogeia Trichomanes*.

It is a widely-spread notion that the pro-embryo of mosses, irrespective of its entirely different physiological nature, is distinguishable from the prothallium of ferns by the fact that the former consists of confervoid cellular threads, the latter of an ulva-like cellular superficies. I was much surprised, therefore, when I found that certain crisped vegetable formations resembling the prothallia of the Equiseta or plants of *Anthoceros punctatus* and which had grown as weeds amongst some unsuccessful sowings of *Lycopodium Selago*, proved to be the pro-embryos of a moss, *Sphagnum cuspidatum*.

Schimper ('Rech. sur les Mousses') has figured the ramified rows of cells which are the first products of the development of Sphagnum-spores when sown in water. Afterwards the same observer noticed certain shoots proceeding from short lateral branches, during the vegetation of the pro-embryo in water. These shoots are very probably the rudiments of leafy branches. When germinating upon moist earth, one of the ramifications of the thread-like pro-embryo becomes a cellular superficies (Pl. XVIII, figs. 6, 8). The disposition of its cells fluctuates between an arrangement in pairs and a simple cross-bar arrangement; this is caused by the repeated division of a single apical cell, by means of septa perpendicular to the surface, turned alternately to the right and to the left. The former kind of cell-succession usually prevails. The copious ramification of the pro-embryo appears sometimes truly, sometimes spuriously, dichotomous; it is rendered indistinct by the appearance of numerous adventitious basal shoots. A vigorous pro-embryo forms a tangled tuft which it would be lost labour to attempt to reduce to any regular system of ramification (Pl. XVIII, fig. 5).

Two phenomena distinguish these pro-embryos in a remarkable manner from the prothallia of ferns and Equisetaceæ. The crisped cellular surfaces are single throughout their whole extent even after ten months' growth. The parenchymatal tissue, from which the female organs of reproduction are produced in the green prothallia, is never seen. The base and the side-edges of the lobes of the pro-embryo are furnished with thread-like processes which are

branched and divided by septa, differing herein considerably from the simple radical threads of prothallia. Such of the above-mentioned processes as are rich in chlorophyll are divided by septa perpendicular to the longitudinal axis; those which are deficient in chlorophyll, by oblique septa. These widely-creeping cellular threads have the capacity of producing new expanded pro-embryos, by enlargement and division of the terminal cells.

In individual cells of the lobes of the embryo, usually in those very near the base, a multiplication commences differing essentially in direction and in kind from that hitherto spoken of. A hemispherical knot of cellular tissue is produced, which by degrees becomes cylindrical, and which, developing, as it does even at an early period, some rudimentary leaves, may be recognised as the shoot of a moss (Pl. XVIII, fig. 10). The arrangement of the cells of the leaves brings to mind Sphagnum; a suspicion which is reduced to certainty by the characteristic thickening layers of the leaf-cells which appear in the fifth leaf. I find the phyllotaxis to be from the beginning $\frac{3}{8}$ (Pl. XVIII, fig. 10). Rootlets springing from the leafy root are not to be found in *Sphagnum acutifolium*.

Hedwig's observations* were the commencement of an accurate knowledge of the sexual reproduction of mosses. He pointed out the antheridia as the male organs, recognised their structure, and observed the escape of their contents. He figured the archegonia as flask-shaped bodies, closed when young, and afterwards opening at their apex. He also pointed out the conversion of the ventral portion of the archegonium into the calyptra, and the formation of the fruit-rudiment within it. Lastly, he showed by experiment that the spores of the mosses are their true seeds. He sowed the spores of *Gymnostomum pyriforme*, and observed their germination, and the development of the inner spore-membrane into a cellular thread, or, as Hedwig called it, a cylindrical cotyledon (l. c., 153, pl. xvi, fig. 9). After some time scales were seen on these threads, which scales, when examined with the microscope, proved to be young plants, the bases of which were attached to branched pro-embryonal

* 'Theoria generationis,' ed. ii, p. 134, *et seq.*

threads. The same was the case with *Funaria hygrometrica*. The production of leafy plants out of pro-embryonal threads was considered by Hedwig's followers to arise from the amalgamation of several threads of the pro-embryo, so as to form the leafy stem (see Schleiden, 'Grundzuge,' 2nd edit., vol. ii., p. 66), an error which was grounded upon the fact that numerous cells of the base of the young leafy plant usually grow into new pro-embryonal threads, the *Brutkeimfäden* of Nägeli. Nägeli clearly explained the development of the leafy axis out of the pro-embryo. He showed* that at the commencement of the formation of the moss-stem, the terminal cells of individual branches, or of the principal axis of the spores or brood-germ-threads, expand, and, through division by means of septa inclined in different directions, become converted into a cellular body, which afterwards produces leaves, and thus indicates the rudiment of a stem. The results obtained by Nägeli have been extended by P. W. Schimper ('Rech. sur les Mousses,' Strassburg, 1848, ss. 1—4) to such a number of different species, that there is no doubt of their general application.

The spermatozoa of the mosses, and (with the exception of an imperfect observation of Bischoff's,) of the cryptogamia generally, were discovered by Unger in 1834 ('Flora,' 1834, p. 145; more fully in 'N. A. A. C.,' xviii, pp. 2, 690, 790). Unger describes the spermatozoa as consisting of a thick body, and a thin thread-like prolongation, which goes in advance when the body is in motion, and is of a spiral form.† The motion of the spermatozoa

* 'Zeitschrift f. wiss. Bot.,' 2, 168.

† 'Bischoff, Kryptog. Gewächse' (Nurnberg, 1828), p. 13 note, mentions that he has always noticed in freshly-opened globules (antheridia) of *Chara hispida*, a medley of numberless infusoria. They appeared to consist of small dark points, which were connected by transverse lines like little strings. They exhibited a continuous tremulous motion, by means of which the individual points, with their stems, revolved round one another. Bischoff was doubtful whether these "infusoria" originated from cellular threads in the interior of the antheridia. It is hardly necessary to remark that Bischoff's dark points are only the optical sections of the turning points of the spiral spermatozoon. Schmidel's observations on Fossombromia (Ic. pl., p. 85) and those of Nees v. Esenbeck ('Flora,' 1822, p. 34) on Sphagnum afford still less claim to the discovery of the Spermatozoa, inasmuch as both observers only saw the motion o. the escaped contents of ruptured antheridia, but did not distinguish the forms of the motile bodies.

is accompanied by continual revolution of the body round its own axis: that is, round the axis of the spiral. Before maturity the spermatozoa are enclosed in quadrangular cells. Later observations have only added one fact to those of Unger, viz., that the thin fore-end of the spermatozoon bears two long oscillating cilia (Thuret, 'Ann. Sc. Nat.,' ii Ser., vol. xiv, p. 68, and iii Ser., vol. xvi, p. 73; Schimper, 'Rech. sur les Mousses,' pl. xv, figs. 25—29; 'Mém. sur les Sphaignes,' pl. viii, figs. 23—25). Unger noticed the cuticle of the antheridia of Sphagnum, but could not decide whether the structureless membrane, which is capable of being detached from the chlorophyll-bearing cells of the covering layer, was on the outside, or on the inside of those cells. He was inclined to assume the latter. Schleiden seems to have fallen altogether into the mistake of supposing the cuticle to be the membrane of a large central cell of the antheridium surrounded by the covering layer, for he alleges ('Grundzüge,' ed. iii, p. 577), that this organ in Sphagnum is a stalked oval sac, formed of a large central cell, and a surrounding cellular layer. This erroneous statement has been entirely refuted by P. W. Schimper ('Rech. sur les Mousses,' p. 52), by means of the history which he gives of the development of the antheridia, and also by his accurate description of the anatomical structure of these organs when they are mature and ruptured.

In the same manner as he has done in the case of the antheridia, P. W. Schimper has recognised the rudimentary formation of the archegonia, by means of the division, by septa inclined in different directions, of an outwardly-protruding papillary cell of the external surface of the apex of the stem. This division is continually repeated in the apical cell of the cellular body, as it gradually becomes cylindrical.

Until the publication of my observations, however, the continental botanists attained no greater knowledge of the structure of the archegonium when ready for impregnation, than was possessed by Hedwig.

In the mean time, in the year 1833, Valentine had discovered the simple rudimentary cell of the moss-fruit, in

the interior of the archegonium ('Trans. Linn. Soc.,' vol. xvii, p. 465). He succeeded in detaching this cell (p. 466). He recognised it also in archegonia, whose apices were still closed, but failed to discover it in Bryum roseum, which in England often bears healthy archegonia, but rarely fruit. He describes the development of the rudimentary cell of the fruit as follows. "Soon after the opening of the upper extremity of the style, another cell is formed on the upper surface of the first. The two adhere firmly, and may be dissected together. Presently another cell is formed, either on the upper surface of the second, or on its side; then appears another, and so on. * * The base of the style increases not by distension, but by addition of fresh matter. * * The fusiform mass within passes its conical extremity deeper and deeper into this tissue, until at last it reaches the branch itself." Valentine observed further that after the separation of the calyptra from the vaginula, the seta increased in growth only at the apex, and he figures accurately the separation of the outer capsule-wall from the inner, by the formation of an annular intercellular space.

Strange to say these observations of Valentine have remained to this day wholly unknown in Germany and France. They are not mentioned by De Candolle ('Organographie végétale,' ed. ii, vol. ii, p. 146); Treviranus ('Pflanzenphysiol,' vol. ii, p. 46); Meyen ('System d. Pflanzenphys.,' vol. iii, p. 385); Schleiden ('Grundzüge,' ed. ii, vol. ii, p. 68); or P. W. Schimper ('Rech. sur les Mousses,' p. 67). I was myself ignorant of them when I published my observations upon the subject in 'Botan. Zeit.,' 1849, p. 798, and in the 'Vergleichende Untersuchungen,' p. 69. Mohl in Wagner's 'Handwörterbuch der Physiol,' vol. iv (1853), p. 279; P. W. Schimper, 'Mem. sur les Sphaignes (1859), p. 10; and Gottsche, 'Botan. Zeit.' (1858), supplement, p. 42, make no mention of Valentine's discoveries. Valentine himself was far from appreciating the importance of his own observations. He expressly disputes Hedwig's views of the sexuality of mosses. He says "If sexes are to be found in mosses they must be sought in the theca

(l. c., p. 777). The sporules of mosses and of all cellular plants are analogous to the pollen of the vasculares." I can claim as my own the account of the origin of the germinal vesicle, of the dependence of its development upon the fact of its impregnation, and the proof of the conformity between the process of formation of the moss-fruit, and that of the embryo of the vascular cryptogams, of the Coniferæ, and of the phanerogamia.

The first accurate account of the development of the moss-capsule was given by H. v. Mohl, ('Flora,' 1833, p. 1; 'Vermische Schriften,' p. 72). He places in a very clear light the relation of the columella of *Sphagnum gracile* to the two walls of the capsule, of the apophysis, and of the peristome. The original homogeneity of the cellular tissue of the young, few-celled fruit-rudiment, has often been noticed by Bischoff (*e. g.*, in 'Nova Acta,' vol. xvii, p. 917). The development of the spores in fours in one mother-cell, was pointed out by Mohl (l. c., p. 72). Lantzius-Beninga showed ('De evolutione sporidiorum in capsulis muscorum,' Göttingen, 1844, pp. 7, 11, 17), that a single annular cellular layer of the interior of the capsule represents the primary mother-cells of the spores, and that the mother-cells, in which the spores originate, are formed out of these primary mother-cells, by their repeated division into two parts. He recognised, in many instances, the free state of the mother-cells within the primary mother-cells, as for instance, in *Orthotrichum speciosum*, *Trichostomum pallidum*, and *Gymnostomum pyriforme;* and he discovered that the membrane both of the primary mother-cells and of the mother-cells became blue with iodine. In a later work, 'Bot. Zeit.,' 1847, p. 17, and more clearly in 'Nova Acta,' vol. xiv, the same observer gives an admirable account of the anatomical structure of the perfect moss-capsule, especially of the peristome, which up to that time had been almost entirely misunderstood. Lantzius-Beninga stated that the teeth of the peristome (except in Splachnum and Polytrichum,) do not consist of perfect cells, but that during the development of the peristome-teeth, a partial thickening occurs in the walls of the cells belonging to a conical

enveloping layer found in the interior of the upper conical part of the capsule, within and beneath the layers which afterwards fall off in the form of the operculum. The thickening of the cell-membranes always occurs on both sides. When a thickening takes place in the outer wall of a cell which is occupied in forming the peristome, then a portion, exactly corresponding in extent and form, of the inner wall of the cell adjoining it on the outside becomes thickened. When the thickened portion of the peristome-cell is found on the wall which is directed towards the axis of the capsule, then the corresponding portion of the outer wall of the neighbouring cell adjoining it on the inside, is thickened in like manner. These thickenings have usually the form of longitudinal stripes, and are so arranged in each of the cells which help to form the peristome, that they look like direct prolongations of the stripes of the wall of the cell next below. When the thickenings of the peristome-cells fill up the adjacent angles of two laterally adjoining peristome-cells which are bounded on the outside or on the inside by a cell of double width, then the thickening of the wall in this wide cell occurs in the form of a median stripe, which has the width of the two corner stripes of the smaller neighbouring peristome-cells. In the formation of the teeth of a moss with a single peristome the outwardly-directed walls only of the peristome-cells (and the corresponding mural stripes of the cells adjoining on the outside) are partially thickened. In mosses with double peristomes the inwardly-directed walls of the peristome-cells are also thickened. When the capsule becomes mature, the cell-walls which have remained unthickened become torn during the separation of the operculum from the capsule, and the thickened longitudinal stripes remain as the peristome teeth. In Splachnum and Polytrichium the peristome-cells are thickened on all sides; in Splachnum however the thickenings are irregular, those which are directed outwards being much the strongest.

Some interesting observations of Bruchs have very lately been published. Gumbel's observations have shown the occurrence of abnormal fruit in mosses ('Nova Acta,' vol. xxiv, p. 652). Those portions of the latter observations which

relate to the production in *Mnium serratum* of two capsules upon one seta, and of two capsules upon one apophysis in *Bryum argenteum*, and *Splachnum vasculosum*, seem to indicate the possibility of a bifurcation of the growing upper end of the fruit-rudiment. Those portions which relate to the discovery of two fruits and two fruit stalks underneath one common calyptra in *Polytrichum juniperinum* and of two stalked fruits upon one seta in *Hypnum plumosum*, appear to point to the existence in the central cell of one and the same archegonium, of two germinal vesicles capable of impregnation. There is hardly a doubt of the occurrence of such a polyembryony, the development of which however must assume a different form, when it is considered that (l. c., p. 653) the case of an amalgamation of two capsules, each furnished with a peristome, has been observed in *Hypnum lutescens*. The mouths of the two capsules are turned to one another, the smaller one having grown up upon the larger one. Both are united by a median process.

In order to arrive at a perfect proof of the sexuality of mosses, it is desirable that hybrids between different species should be artificially produced: *i. e.* that fruits should be obtained by the impregnation of the archegonia of one species by the antheridia of another. Bayrhoffer suggested that some mosses found by him growing wild were hybrids between *Gymnostomum pyriforme* and *fasciculare* on the one side, and *Funaria hygrometrica* on the other side (see Braun's 'Verjüngung,' p. 330). I have not yet succeeded in producing such hybrids experimentally, although I brought together antheridial plants of *Gymnostomum pyriforme* and plants of *Funaria hygrometrica* with their antheridial shoots cut off. The mutilated plants of *Funaria hygrometrica* always perished. This is however no reason for giving up the attempt. By changing the method of cultivation the right one will probably be attained at last which will lead to the desired result.

CHAPTER VII.

FERNS.

1. *Their germination.* — The spores of ferns usually exhibit a tolerably thick, brittle, outer membrane, which is furnished with prominent linear markings, or with wart-like protuberances. When exposed to moisture and warmth the inner membrane swells and ruptures the brittle outer shell: this rupture usually occurs at the point of junction of those three prominent lines of the outer membrane which correspond with the lines of contact of the spore with the three sister-spores which originated in the same mother-cell and which, with the spore, formed a tetrahedron. In the spores of those species in which the spore-mother-cell divides into four cells having the form of quadrants of a sphere and lying in one plane (which spores when ripe have the shape of an elongated kidney) the exosporium usually bursts by a longitudinal fissure, the course of which in like manner corresponds with the line of contact of the spore with its sister spores; as for instance in *Platycerium alcicorne* (Pl. XXIV, fig. 1). A portion of the inner membrane protrudes through the fissure of the exosporium, and some chlorophyll-bodies are formed in this protruded portion. The latter is soon afterwards separated by a partition from that portion which remains inside the outer membrane. In the outer of the two newly formed cells the transverse division is repeated; it usually occurs several times (from three to five) in the terminal cell, so that the young prothallium is converted into a row of cells (Pl. XXIV, fig. 1). Sometimes the undermost cell, the one which adjoins the exosporium, becomes considerably elon-

gated; as may be observed in *Asplenium septentrionale* (Pl. XXIV, fig. 3). In most cases however this elongation does not occur. I have never seen it in *Pteris aquilina*, *Aspidium filix-mas*, Ceratopteris or Adiantum. In those species where considerable elongation of the lowest cell occasionally takes place, it seems to be caused by deficiency of light. The first rootlet is produced during the continuance of the transverse division of the terminal cell of the young prothallium: it has the form of a cylindrical process developed from a protrusion of the membrane of the lowest, more rarely of the second lowest, cell of the prothallium. The rootlet very soon after its appearance is separated from the original cavity of its mother-cell by a septum convex towards the interior (Pl. XXIV, figs. 1—3). After about the fifth transverse division of the apical cell of the young prothallium, this cell divides by a longitudinal septum. The two apical cells afterwards divide frequently by transverse septa. In the cells of the second degree which are thus formed transverse septa are produced. The formation of these septa is however usually suppressed in the two or three first-formed lowermost pairs of cells and often also in one of the two next equal-aged cells (Pl. XXIV, fig. 2). Thus the prothallium begins to be converted into a cellular surface. At the same time the direction of its growth is turned more and more from the light, so that it soon assumes a position parallel to the surface of the ground: when the light is powerful it adheres closely to the earth.*

The apical cells often divide also by longitudinal septa, which diverge slightly from the longitudinal axis of the prothallium, and which, like all septa which are produced during the early growth of the organ, are perpendicular to its surface. The prothallium has now four apical cells, of which the two outer ones grow more rapidly in length than the median ones, and immediately divide repeatedly by

* The turning away of the prothallium from the light, by which the fore edge of each prothallium is continually diverted from the source of light, was first observed by Wigand ('Beiträge zur Botanik,' 1854, p. 35). His explanation however is altogether erroneous; he assumes that the upper surface of the prothallium was drawn from the light. If this were so the prothallium must turn itself to the light.

septa cutting those which diverge from the longitudinal axis of the organ at an angle of about 45° (Pl. XXIV, fig. 3). By this means the foundation is laid for the two-lobed form of the prothallium. The cells of the edge of the wings of the fore end of the prothallium then divide very frequently by septa parallel to the chord of the arc of their circumference. After a series of such divisions there are produced in the marginal cells, longitudinal septa at right angles to the latest formed transverse septa. This cell-multiplication, by which both lobes of the prothallium are rapidly and remarkably enlarged, is least active on the outside of the lobes, where it soon ceases. The cessation progresses from the hinder part of the prothallium to the apex of each of the side lobes. On the other hand those cells of the two lobes which are directed towards the deep indentation of the fore edge, continue to multiply for a longer period. The multiplication, however, is most active in the two cells which occupy the base of the notch between the two wings of the prothallium, which notch is constantly increasing in depth. These cells divide continually and repeatedly by means of transverse septa at right angles to the longitudinal axis of the prothallium, alternating with divisions by means of longitudinal septa which converge slightly to the longitudinal axis. Those of the new cells thus formed which are farthest from the middle point of the indentation begin immediately to diverge in their growth from the longitudinal axis of the prothallium to the extent of about 65°. By this means the new cells thus produced drive the cells adjoining them on the outside upwards and outwards. During their change of position the growth of these cells diverges more and more from the longitudinal axis of the prothallium, ultimately to the extent of 90°. Those daughter-cells which are separated from the cells in the lowest portion of the indentation push themselves upwards laterally by the side of their mother-cells, by means of an innate power of growth. Whilst they push the adjoining older cells outwards, they take part in the formation of the two side wings of the prothallium, which consequently increase continually in size and in the number of their cells, notwithstanding the progressive cessation of the multiplication

of the cells of their outer edge (Pl. XXIV, fig. 6). The apical cell for the time being of the wing of the prothallium, is continually pushed downwards and outwards and replaced by a younger one. The growth of the youngest cells in the direction diverging from the longitudinal axis of the side wings is frequently more active at their inner than at their outer end. Where this phenomenon is very strongly manifested it leads to such a remarkable development of the breadth of the two wings of the prothallium that the one overlaps the other. This circumstance however occurs, for the most part at least, only in prothallia of exuberant growth; it does not take place until the termination of the normal growth of the prothallium.

Individual cells of the under side of the prothallium protrude outwardly in a hemispherical form. In very young prothallia, or in thin shoots of old exuberant prothallia, the same thing occurs in the marginal cells (Pl. XXIV, fig. 4). The development of these cellular excrescences usually commences at the hinder part of the prothallium, proceeding from thence towards the front part, but without any very great regularity. As a rule one excrescence only is developed on one cell of the prothallium. In the median line of the latter, one of these excrescences is produced from almost every cell; towards the sides their number diminishes, and at the edges of the wings of the prothallia the formation is entirely suppressed. Their expansion coincides with that of the radicular appendages. The protruding portion of the free outer surface of the cell is soon separated from the primary cell-cavity by a transverse septum. This transverse division is often repeated a second time, more rarely several times, so that the hemispherical terminal cell of the excrescence is supported by one, or by several, discoid shortly cylindrical cells. The nature of their contents differs little at first from that of the vegetative cells of the prothallium. The walls are covered by a layer of chlorophyll having somewhat smaller granules than that of the neighbouring cells; their supply of protoplasm is somewhat larger. From this period the highly refractive protoplasm of the young antheridium accumulates to such an extent, that the arrangement of its component cells is very difficult

to recognise. There can however be no doubt that after some time the antheridium is composed of a cylindrical or angular, almost cubical, central cell of large size, very rich in granular protoplasm, supported by one cylindrical or two semi-cylindrical cells, covered by a cell having the form of a segment of a sphere, and surrounded laterally by a girdle, which in most cases looks at first sight like a simple annular cell, or two such cells standing one over the other, but which, after more careful examination, and especially after treatment with a saccharine solution and iodine, may often be seen to be composed of several cells, from two to four in number, lying in one plane.

Those states of the antheridia which, judging from their size and their position on the prothallium, are intermediate between the condition just mentioned and the unicellular condition, may be distinctly recognised by the sharply defined, circular boundary line of the apical cell; and, less distinctly, by the appearance of the central cell which is rich in protoplasm. In some young antheridia the best object-glasses especially when combined with the use of a solution of sugar and iodine exhibit the lines of contact of the cell-walls with the outer surface of the antheridia. These lines run obliquely downwards, usually in a left-handed spiral which describes about a sixth part of a circumference (Pl. XXIV, fig. 9). The analogy to be derived from the process of development of the antheridia of the Muscineæ renders it probable that the large central cell is formed by the production of an excentrical, inclined, longitudinal septum in the young antheridium, followed by the production of another excentrical septum cutting the latter at right angles, and the subsequent formation of a longitudinal septum cutting both the above at an angle of 45°, such formation taking place after the apical cell of the antheridium has been isolated by a strongly inclined almost horizontal septum cutting the primary longitudinal septum. Where the central cell is surrounded by *two* zones of enveloping cells it is manifest that the two zones originate in the transverse division of the primary single zone.

The structure of the prothallia and antheridia of all the Polypodiaceæ which have been yet examined is identical in

all essential points. The only specific differences are, that in certain species (such as *Aspidium filix-mas*, and several species of Adiantum) certain marginal cells of the prothallium grow into papillæ, which in Aspidium are thin and cylindrical with a clavate end, and in Adiantum are very large and flask-shaped, whilst in the prothallia of other ferns the margin is destitute of such protuberances, as is the case in *Pteris aquilina* and *serrulata*. The only known instance of variation is afforded by *Ceratopteris thalictroides*. When the large spores of this species germinate, and the exosporium bursts, it is seen that the portion of the prothallium which is enclosed within the lobes of the exosporium, is a multicellular roundish body. The conclusion from this fact is that the inner cell of the spore is divided into several daughter-cells before the bursting of the exosporium. The prothallium moreover does not develope two lateral lobes with a deep indentation between them, having the focus of continuous cell-multiplication, at its base, but the point of most active cell-multiplication is situated sideways on the prothallium (Pl. XXIV, fig. 16). One wing only of its fore edge is developed. The rudimentary cells of the antheridia are for the most part marginal cells of the prothallium somewhat deeply buried between the vegetative cells of the margin. The process of cell-division in them coincides with that which is supposed to exist in most of the Polypodiaceæ (Pl. XXIV, figs. 17—19).*

* Wigand states that the mother-cells of spermatozoa, and even motile spermatozoa themselves, are sometimes found in the chlorophyll-bearing vegetative cells of the prothallium. This statement has not been confirmed by any other observer. Wigand has probably seen appearances which I have myself met with, though on rare occasions. I have found in many of the vegetative cells of old, abnormally developed, prothallia, globular or elongated, sharply defined masses of a thick mucilaginous substance which for the most part hung together in arborescent ramifications, but were to some extent detached, and formed entirely free globular bodies. The diameter of these bodies is but little (about a third) greater than that of the mother-cells of the spermatozoa. They were present in individual cells sometimes in greater sometimes in less numbers. The arrangement of the chlorophyll of the cells in which they were enclosed was not materially disturbed although the colour of the chlorophyll was slightly faded. Some of the arborescent groups were drawn out at one end into a thin thread-like cell which had quite the appearance of a fungoid filament, and which was attached at its extremity to the free outer wall of the cell of the prothallium. In other cells of the same prothallium the chlorophyll had disappeared and they were filled with empty cells having a firm membrane and looking like the mother-cells of zoospores. These structures are certainly

The cells of the antheridia, which surround the central cell, do not multiply any further. The latter, however, after a considerable increase of its circumference, is transformed by a series of divisions into a globular group of cubical cells (Pl. XXIV, figs. 10, 11). By the growth of this cellular mass the cells of the covering layer are extended more and more into a tabular form, sometimes to such an extent, that their cavities are entirely obliterated. During the multiplication of the central cell their fluid contents have become as clear as water.

In each of the small tesselated cells within the antheridium there is produced a flat spirally twisted spermatozoon in the interior of a lenticular or globular vesicle, the latter being apparently the primary nucleus of the small cell. The turns of the spiral are but few in number.

As the antheridium approaches maturity the walls of the small internal cells are dissolved and the vesicles enclosing the spermatozoa then lie free, enveloped in a granular mucilage, and surrounded by the compressed covering cells. If the antheridium is now exposed to moisture, its contents swell, the flatly compressed cell of the apex bursts in the middle in a stellate manner, and the vesicles enclosing the spermatozoon escape through the fissures. If the spermatozoa are fully-formed and ripe, the vesicles when lying in water, exhibit a rotatory motion shortly after their escape from the antheridium. I have often observed that at the commencement of this motion, one of the ends of the spermatozoon (usually the fore-end, which is the thicker one and bears the cilia), protrudes from a fissure in the vesicle. Suddenly the vesicle bursts by a wide opening, the spermatozoon becomes free, and shoots out from it in very rapid motion.

The expanded fore-end of the spermatozoa, as has been mentioned, is compressed laterally to a considerable extent; the outer side of its spiral coils bears numerous delicate cilia, which vibrate actively during its motion (Pl. XXIV, figs. 13, 15). At the opposite end the spermatozoon gradually fines off into a very long hair-like termina-

always foreign to the prothallium and are probably states of development of an entophytal fungus.

tion. The latter often retains its original spiral form, and remains attached to the interior of the vesicle within which the spermatozoon originated (Pl. XXIV, fig. $14^{a,b}$). The forward motion of the spermatozoon is always accompanied by a rapid rotation round the axis of the spiral, and follows the direction of this spiral, which is sometimes a right-handed, sometimes a left-handed one.*

When the prothallium has become two-lobed, and has a deep indentation on its fore-edge, the cells of that portion of it which lies immediately behind the indentation, divide by means of septa parallel to the surface of the prothallium. This division is repeated two or three times, always in the lower one of the newly-formed cells. By this means a flat cushion of cellular tissue is formed on the under side of the prothallium. On its hinder part, new antheridia continue to be formed for a considerable time. The archegonia are produced at the fore-part adjoining the indentation.†

The mother-cell of an archegonium is distinguished from the adjoining cells by an abundance of finely granular mucilage, and by the presence of a larger less flattened nucleus. The adjoining cells just mentioned are rich in chlorophyll: their contents are clear like water, and they have a small lenticular nucleus adherent to the cell-wall.

* The statements of authors with regard to the form of the spermatozoa of Ferns, their number, their nature, and the mode of attachment of their cilia are in some respects very contradictory. Their discoverer, Nägeli, makes no mention of cilia. Leszcyc-Sumiuski in his account of the development of Ferns (Berlin, 1848) speaks of a few large cilia as attached to the clavate fore end of the spermatozoon of *Pteris serrulata*. This is an error, as the spermatozoa of the latter species are similar to those of Asplenium. Schacht ('Linnæa,' Bd. xxii) considered the vesicle in which the spermatozoon is produced, and which is often dragged along by the whip-shaped end of the latter, to be an essential portion of it. This accounts for the difference between his observations and those of other botanists. He considered the vesicle to be the fore end of the spermatozoon and that the hinder part preceded the narrower ciliated coils when in motion. Thuret's statements ('Ann. des Sc. Nat,' iii ser., vol. 14) agree with mine except that he does not mention the tail of the spermatozoon.

† In order to justify the application to the organs of Ferns, of an expression hitherto only used when speaking of the female organs of mosses, I must refer to a subsequent part of this work; where I endeavour to show that the fruit (capsule and fruit stalk) of a moss answers to that which in ferns (taken in the most extended sense) is simply called the plant; and that the prothallium of the fern is equivalent to the moss-stem, bearing antheridia and archegonia, which is often much branched.

The hinder end of the spermatozoon is frequently drawn out into a narrow prolongation, but this is not a constant character. It arises probably from the fact that during the parting asunder of the spermatozoon and its mother-cell, the plastic substance of the spermatozoon remains attached to the membrane of the latter cell, and is mechanically drawn out into a thin filament, which eventually breaks off.

The first division of the primary cell of an archegonium can only be seen by means of careful transverse sections of the prothallium made perpendicularly to its surface. The cell divides into an inner and an outer daughter-cell by means of a septum parallel to the free outer surface. The former becomes the central cell of the archegonium—the embryo-sac. At a later period it is the place of formation of the embryo. The neck of the archegonium is produced by the multiplication of the outer cell (Pl. XXV, figs. 1, 2). This cell protrudes outwardly, and is divided into two daughter-cells by a septum strongly inclined to the surface of the prothallium, and often almost perpendicular to it. This septum is sometimes at right angles to a plane passing through the longitudinal axis of the prothallium, sometimes it forms an acute angle with that plane, and sometimes it is parallel to it. One of these positions is as frequent as the others. The larger of the two daughter-cells is divided anew by a septum super-imposed upon the latter septum, and inclined in an opposite direction. The two-surfaced wedge-shaped apical cell then divides from four to ten times by means of septa inclined in different directions (Pl. XXV, fig. 2). With this process the longitudinal growth of the organ terminates. Each of the cells of the second degree—which cells originate in the division of the apical cell by a septum parallel to one of the lateral surfaces—divides immediately after its production, by means of a longitudinal septum radiating from the axis of the archegonium. The neck of the archegonium consequently consists of four parallel longitudinal rows of cells. Each of the cells contains a lenticular nucleus, lying close to the cell-wall, and from which strings of granular protoplasm radiate. Granules of a firm consistence are dispersed throughout the

protoplasmic covering of the cell-wall. These granules are usually very few in number; sometimes however they are more abundant, and they are not unfrequently furnished with a thin coating of chlorophyll.

The necks of the archegonia when perfect frequently exhibit a central string of cells in their longitudinal axis (Pl. XXV, figs. 3, 5, 6). The position of the cells of this fifth longitudinal row relatively to those of the four surrounding rows, leads to the conclusion that the axile row of cells is formed by the division of the cells of one of the primary longitudinal rows into three-sided outer and four-sided inner cells by means of septa parallel to the chord of the arc of the free outer surface; a process analogous to the development of the axile string of cells in the neck of the archegonia of liverworts and mosses. This formation of axile cells frequently does not extend throughout the whole length of the organ. It is sometimes suppressed in the cells immediately adjoining the embryo-sac (Pl. XXV, fig. 5). More rarely it occurs only in the latter cells, in which case the upper part of the neck of the archegonia consists of four, and its lower part of five rows of cells. Immediately after the formation of the axile string, the contents of the cells are found to be of a grumous nature, and the transverse septa which separate the individual cells are soft and gelatinous. When treated with a solution of glycerine, or with any substance which abstracts water, the cells become contracted, and form granular mucilaginous matter, sometimes in separate spherical lumps, sometimes in the shape of a single vermiform body (Pl. XXV, fig. 8). I attribute the formation of the similar masses which occur in the canals of the necks of archegonia which are approaching maturity, to a similar transformation of the axile string during the further normal development of the archegonia (Pl. XXV, fig. 11).

Quite as often however, or even oftener, the formation of an axile row of cells in the neck of the archegonium is suppressed. Both forms of archegonia occur upon prothallia of the same species, and even upon one and the same prothallium. The one form is as common as the other in *Pteris serrulata* and *Ceratopteris thalictroides*. In *Aspi-*

dium filix-mas and *Gymnogramma calomelanos* the first-mentioned form is more frequent. This form answers to the structure of the archegonia in liverworts and mosses, the other corresponds with that of the archegonia of the Equisetaceæ, Rhizocarpeæ, and Lycopodiaceæ. Ferns constitute the intermediate link between these groups, so far as regards the organization of the female reproductive apparatus.

During the longitudinal development of the neck of the archegonium it bends backwards from the indentation of the fore edge of the prothallium. The amount of curvature varies slightly in the archegonia of the same prothallium. The archegonia of prothallia which bear those organs on both sides are bent in the same direction, those of the upper surface being usually more curved than those of the lower surface. The curvature is very considerable in the necks of the archegonia of those prothallia which are not close to the earth, but which (in consequence of their growing in masses) have become diverted obliquely upwards. Thus it would seem that the curvature of the necks of archegonia affords another instance of negative heliotropismus, *i. e.*, of the turning away of an organ from the rays of light.

The number of archegonia is far less than that of the antheridia. On normally developed prothallia which contain an embryonal rudiment, there are seldom more than eight. The development of the archegonia commences close behind the indentation of the fore edge of the prothallium, and progresses from thence both forwards and sideways during the continuance of the growth of the prothallium.

In some prothallia, when growing under a sufficient exposure to light, the rudimentary cells of the archegonia are always on the under surface of the prothallium. Prothallia however of the most different species, when growing erect in closely packed tufts, or in places where few rays of light penetrate, develope archegonia on both surfaces. On the upper surface, which is usually distinguishable by the paucity or absence of rootlets, the archegonia are usually mixed with antheridia. It is evident that shade is

favorable to the production of sexual organs as well as of roots.

In *Ceratopteris thalictroides*, the antheridia of which are abnormal in position and structure, prothallia occur having numerous cushion-like masses of tissue in which archegonia are produced, each one of such cushions being situated behind one of the numerous indentations of the edge of the prothallium.

At an early period, even before the complete formation of the neck, a secondary free nucleus appears in the upper part of the central cell of the archegonium. The large primary nucleus of the central cell is still present. The secondary nucleus is soon seen to be surrounded by a free spherical cell, in close proximity with the internal surface of the apex of the central cell (Pl. XXV, figs. 5—9). This is the germinal vesicle. When it first appears its diameter is only about one sixth of that of the central cell, but, even before the bursting of the apex of the archegonium, it grows, to almost one half the size of its mother-cell. For some time after its appearance the primary nucleus of the central cell remains unchanged (Pl. XXV, figs. 3, 5, 8): at a later period it disappears; this takes place before the opening of the apex of the neck of the archegonium (Pl. XXV, figs. 4, 7, 11).

The cells of the inner tissue of the prothallium which are adjacent to the central cell of the archegonium, divide repeatedly by septa at right angles to the bounding surfaces, and by this means are converted into a kind of epithelial layer, consisting of narrow cells containing a quantity of finely granular protoplasm (Pl. XXV, figs. 3, 5, 11). The period of the commencement, and the intensity of this multiplication, are very different in individual instances. (Compare Pl. XXV, fig. 3, with Pl. XXV, figs. 4, 7.)

During the formation of the germinal vesicle a wide canal leading to the embryo-sac is formed in the longitudinal axis of the neck of the archegonium. The apex of the neck of the archegonium remains firmly closed during the development of this canal. In most cases during the progress of this development, the cells of the

arch of the apex of the archegonium multiply by division which takes place by means of septa at right angles to the outer surfaces. This process is especially remarkable in *Gymnogramma calomelanos* (Pl. XXV, fig. 7). Where the neck of the archegonium consists of only four longitudinal rows of cells the axile canal is manifestly formed by the parting asunder of the angles of contact of the latter cells. The membranes of the cells grow in the direction of tangents to the cylindrical organ: thus an intercellular space originates between them, which is often of considerable width. The process commences underneath the arch of the apex of the archegonium and proceeds from thence to its base (Pl. XXV, fig. 4). When the neck of the archegonium is traversed by an axile string of cells the canal can only be produced by the dissolution of the transverse septa of these cells. In this case also the dissolution is preceded by an increase in growth of the peripheral cells in a tangential direction, which is especially remarkable at the apex of the neck of the archegonium, so that the axile string of cells assumes a clavate form (Pl. XXV, figs. 5, 7).

Within the canal of the neck of the archegonium, whilst the latter is still closed at the apex, there is sometimes (but by no means always) to be found an elongated vermiform body, of a finely granular, tough, gelatinous consistence, club-shaped at the upper, and tapering towards the lower end. At other times there may be seen several similar bodies within the canal, of which the uppermost are usually elongated, and the lower ones spherical. The reverse is however sometimes the case, the lower bodies being sometimes longer than the upper ones (Pl. XXV, figs. 7, 11). These bodies are very probably nothing more than the altered contents of the cells of the axile string of the neck of the archegonium, which upon the dissolution of the transverse septa run together more or less completely into one mass. The elongated clavate form of the upper of these bodies (a form which is of frequent occurrence when several of such bodies are present) probably results from the fact that in this case also the formation of the canal of the neck, the dissolution of the transverse septa of the axile row of cells, and consequently also the flowing together of

the contents of these cells, proceed from above downwards; the process taking place rapidly at first, and afterwards more slowly.

After the formation of the canal of the neck, and whilst the apex of the archegonium is still closed, the walls of the cells of the peripheral layer become arched inwards to a considerable extent, and protrude into the canal: a manifest proof that these cells, being in a state of active expansion, exert a great pressure upon, and displace the fluid contents of the canal. Ultimately the cells of the apex part asunder, by which means a portion of the mucilaginous fluid contained in the canal usually escapes through the opening. By this means individual cells are not unfrequently detached and thrust off (Pl. XXV, fig. 12). The canal is now open externally, and exhibits an uninterrupted communication from without inwards, up to the central cell of the archegonium.

The membrane of the arch of the apex of the latter has in the mean time become softened. A gentle pressure upon the covering glass not only forces the mucilage of the canal out of the mouth of the latter, but a portion also of the contents of the embryo-sac is gradually driven into, and through the canal. The motion however is not so sudden as in the case where the contents of a cell escape through a fissure produced by the bursting under pressure of an elastic membrane. In one case I observed that one of the bodies in the canal had made its way into the central cell; a circumstance which proves clearly the exposed nature of the embryo-sac (Pl. XXV, fig. 11). The membrane of the germinal vesicle on the other hand, even before the bursting of the archegonium, is somewhat firmer. It is clearly seen, when an embryo-sac and the germinal vesicle within it are injured in making a section, that the membrane exhibits folds (Pl. XXV, fig. 9).

Most archegonia are not developed any further. The cell-walls which adjoin the canal, as well as the large cell at the base of the archegonium, assume the purplish-brown colour, which is peculiar to the fading cell-membranes of almost all the higher cryptogams. This is the fate not

only of all except one* of the archegonia of the same prothallium, but by far the greater number of prothallia are entirely abortive, and produce no young plant. It is not too much to say that hardly one prothallium in ten produces a frond-bearing plant. Prothallia which are devoid of embryos, do not, however, by any means die; when they are not deprived of the conditions essential to their vitality, that is to say, moderate warmth, subdued light, and abundant moisture, they continue to develope themselves for several months. In the simplest case the side lobes of the prothallium increase very considerably in size; they overlap one another to a great extent in front of the indentation of the fore edge. The prothallium when growing exuberantly becomes circular; it attains a diameter which is from four to six times larger than that of the prothallia of the same species which have produced young plants. This is the regular rule in abortive prothallia of *Gymnogramma chrysophylla* and others. The cushion of the under-surface grows at the same time in thickness and in length. The latter growth is produced by repeated division of the cells which adjoin the bottom of the slit of the fore edge, and which division takes place by means of septa at right angles to the upper surface of the prothallium. At the same time a number (often a very great number) of archegonia are usually produced upon the prominent cushion of fleshy cellular tissue on the under side of the prothallium. These archegonia, with the rarest exceptions, are all abortive, probably in consequence of the fact that no more new antheridia are produced upon the hinder, oldest portions, of the same prothallium. The earliest of these archegonia have the same form as those which are produced contemporaneously with the latest antheridia. The later ones, however, either develope a rudimentary neck only, or no neck at all. The large central cell and the canal filled with mucilage which leads to it appear to be sunk into the under side of the prothallium (Pl. XXVIII, fig. 2). The obser-

* With the rarest exceptions, such as the case of *Ceratopteris thalictroides*, observed by Mercklin ('Beobachtungen an Prothallium der Farnkr.' Petersburg, 1850) and *Pteris aquilina* and *Aspidium filix-mas* observed by myself.

vation of such archegonia, and the comparison of them with those placed farther backwards and having perfect necks, seems to have led Lesczyc-Suminski, and after him Mercklin, to the erroneous conclusion, that the archegonium in its earliest youth was a short canal opening upon the under side of the prothallium, and that the neck was formed by repeated division, in a direction parallel to the surface of the prothallium, of the cells surrounding the mouth of that canal.

The abortive prothallia of Nothochlæna, Allosurus, and *Gymnogramma calomelanos* often exhibit shoots. The arrangement of the cells of the prothallium of ferns generally resembles that of the leaf-like shoots of Pellia, Riccia, and Marchantia. It might be supposed from this that a new shoot would originate at the bottom of the notch of the fore edge, and that new shoots again would arise in the axils which the last-mentioned shoot would form with the side wings of the fore edge. This, however, is rarely the case (Pl. XVIII, fig. 1). Usually several of the cells of the edge of the prothallium grow into adventitious shoots, which generally have the shape of a large spatula. The activity of the multiplication of their cells breadthwise is exceedingly various. Very slender adventitious shoots with unicellular bases often become detached from their prothallia at an early period by the death and dissolution of the cells attached to them. They then represent independent, very small prothallia (Pl. XXIV, fig. 4), and often bear very numerous antheridia.

The development of a very great number of antheridia is an especial peculiarity which often occurs in the shoots of the prothallia of ferns. They are either entirely barren, or if antheridia are found, the latter are in great multitudes and closely pressed together, there being often as many as a hundred upon one shoot. I have never seen archegonia upon one of these shoots; they certainly have a tendency to produce only male organs of fructification.

Old abortive prothallia of *Gymnogramma chrysophylla* often exhibit a very remarkable appearance in winter. Near the hinder end several small oval knots of cellular tissue are formed; little knots varying from the size of a millet-seed to that of a pea, and consisting of narrow cells filled

with starch and oil-drops (Pl. XXVI, fig. 33^b.) In the earlier stages these knots are whitish or yellowish in colour; afterwards their outer side becomes brownish by the formation of from two to three layers of cork-cells. Perhaps these wonderful organs are gemmæ, destined to reproduce the prothallium.

It may be considered as beyond question that the penetration of a spermatozoon into the open canal of the neck of the archegonium is necessary in order that the spherical cell within the central cell may be further developed, so as to become a frond-bearing plant. Under ordinary circumstances the spermatozoa have the means afforded them of swimming to the opening of the archegonium. Whenever a dew occurs, numerous drops of water are found on the under side of the parenchymatal cushion of the prothallium. The flat space between the prothallium and the ground is often filled with water. Under such circumstances, as the ground becomes gradually drier, air-bubbles are formed under the prothallium, and their presence is shown by the silvery-green glimmer which is exhibited by the tissue above them.

The spermatozoa enter the canal, pass through it, and ultimately reach the interior of the central cell, piercing through the softened membrane of the apex of the latter. Here they move about for some time, sporting actively around the germinal vesicle, which is in close proximity to the inner wall of the central cell near the place of entry of the spermatozoa.* Immediately after the arrival of spermatozoa in the embryo-sac the interior of the mouth of the canal is closed by the transverse expansion of its bounding

* I repeat here, with some additions, the course of observations upon which the above statements are founded, an account of which I have already given in the 'Reports of the Royal Scientific Society of Saxony.'

When a quantity of fern-spores are sown, the germinating prothallia are developed at very different periods. The earliest prothallia produce in the first instance only antheridia, afterwards antheridia and archegonia together, and when advanced in age, only archegonia. The earliest prothallia have already attained the latter stage at the time when the later prothallia, the development of which has been retarded by the shade afforded by the earlier ones, are thickly covered with antheridia. If the plants are now kept for some days rather dry, and then saturated with water, the result will be that numbers of antheridia will emit spermatozoa, and numbers of archegonia will open contemporaneously. The water should not be poured over the plants, but the pot should be placed in water nearly up to its margin, by which means capillary

cells. This process is the first visible effect of impregnation; in abortive archegonia the canal remains open. In the latter the walls of the canal throughout, and also those of the central cell, assume a deep brown colour. In impregnated archegonia this colour only extends downwards over that part of the canal which is not closed. Immediately after the closing of the lower end of the canal, and during the progress of active multiplication in the cells adjoining the embryo-sac, the impregnated germinal vesicle attains the size of the sac. Even before it arrives at this stage two secondary nuclei usually appear in its interior in the place of the primary one which has disappeared (Pl. XXVI, fig. 5). The first septum by which the germinal vesicle is divided, is not however formed until the latter has entirely filled the embryo-sac. This septum stands at right angles to the longitudinal axis of the prothallium, and almost perpendicular to its surface. It diverges from a perpendicular erected upon that surface, downwards and forwards towards the indentation of the prothallium (*a*, *b* in Pl. XXVIII, figs. 1^b, 3^b; Pl. XXVII, figs. 6^b, 7^b). Soon afterwards an oblique septum is formed in each of the two cells into which the germinal vesicle is divided;

attraction and condensation will yield abundance of moisture to the prothallia. After one or two hours the surfaces of the larger prothallia, which are covered with archegonia, are found almost covered with spermatozoa, partly in motion and partly at rest. If a delicate longitudinal section through the parenchyma of these prothallia be examined immediately, with a magnifying power of from 200 to 300 diameters, spermatozoa are sometimes found in all the archegonia along the whole length of the section. I thus found three spermatozoon in active motion in the central cell of the archegonium of *Aspidium filix-mas*. In this case the motion ceased seven minutes after the commencement of the observation, and was accompanied (probably caused) by the coagulation of the albuminous matter of the cell-contents. In the same fern on two occasions, and also in *Gymnogramma calomelanos* and *Pteris aquilina*, I have seen a spermatozoon in motion in the central cell of the archegonium; and in the above-mentioned species, and also in *Asplenium septentrionale*, and *filix-femina*, I have seen a motionless body near the germinal vesicle (after the growth of the latter has commenced) answering in form to a spermatozoon. Lastly, in *Aspidium filix-mas* and *Pteris aquilina*, I have often seen motile spermatozoa in the canal of the opened archegonia, the motion of which spermatozoa ceased during the continuance of my observation. I may add that these observations were very numerous, and were undertaken with the view of following out the cell development of the embryo. In a single prothallium, cultivated in the manner stated above, and laid open longitudinally as I have mentioned, there will not be found more than three, or at the most, four archegonia open at the apex; spermatozoa will probably be found in not more than one in thirty of such archegonia, and they will often not be found at all.

the septum in the hinder cell is inclined downwards and backwards, that in the front cell upwards and forwards. The young embryo now consists of four cells, having the form of segments of a sphere, which fall into a vertical plane passing through the longitudinal axis of the prothallium (Pl. XXVIII, fig. 1). *Pteris aquilina* and *Aspidium filix-mass* exhibit a specific difference in the angles of inclination of the newly-formed septa. The upper angle which the newly-formed septum in the front cell forms with the older one (Pl. XXVI, figs. 6 ^{b}, 7 ^{b}, *b*, *c*) is widely open in *Aspidium filix-mas;* it is almost a right angle; the lower angle of the septum in the hinder cell is very acute (Pl. XXVI, figs. 6 ^{b}, 7 ^{b}, *a*, *d*). In *Pteris aquilina* this state of things is exactly reversed (Pl. XXVIII, figs. 1 ^{b}, 3 ^{b}, *a*, *d*, *b*, *c*). In connexion with this difference there exists also a difference in the further development. In both species the stem-bud and the first frond are formed out of one of the four cells, viz., the lower one of the two front cells (Pl. XXVIII, figs. 1, 3, *a.c*; Pl. XXVI, figs. 6, 7, *a.c*), and the first root is produced from another of those four cells. But in *Aspidium filix-mas* the mother-cell of the root (*b,d* Pl. XXVI, figs. 6, 7) lies opposite to that of the stem; in *Pteris aquilina* it lies at the side (*a,d* Pl. XXVIII, figs. 1, 3). In Aspidium the primary abortive axis of the embryo,* is developed almost exclusively by continual divisions of that one of the four cells which is most distant from the mouth of the archegonium. In Pteris the descendants of the two cells which are furthest from the archegonium compose this organ, which in that genus is much larger (Pl. XXVIII, fig. 3). The fourth cell of the young embryo which lies under the mouth of the archegonium multiplies still further in Aspidium, although only to a slight extent. Its derivative cells do not form a detached portion of the germ-plant, but go to form the cortical portion between the back of the first frond and the first root (Pl. XXVI, fig. 7).

All the vascular cryptograms in which the germination

* The foot-like appendage by which the young fern is attached to the prothallium. Only a few of the cells of the rudiment of the root take part in the formation of this "foot" (Pl. XXVI, fig. 7).

has been observed exhibit the same arrangement of the first four cells of the embryo. This arrangement exists in the Rhizocarpeæ, the Equisetaceæ, and in Isoetes; and the position of the first cells of the rudiment of the germ-plant at the lower end of the suspensor of Selaginella, is the same. In these cases the primary leafless axis is formed principally by the multiplication of the lowest of the four cells; of that one namely which is turned away from the mouth of the archegonium. One of the side cells produces the primary indefinite axis of the plant. A third cell forms the first root, if the embryo produces such an organ. Salvinia is well known to be generally rootless; Selaginella does not send out the first root until after the first bifurcation of the stem. In this prevailing fact there is such a marked difference between the vascular cryptograms and monocotyledons, that the remarkable similarity between the germ-plants of the Naiadeæ and the grasses, and those of the vascular cryptograms (especially such of the latter as have a prothallium devoid of chlorophyll) upon which similarity I once attempted to ground a comparison of the organs of the two families, appears to be an unessential external resemblance.

The multiplication of the primary cell of the lateral principal shoot considerably exceeds that of the mother-cell of the primary axis. The same thing prevails although in a less degree in the primary cell of the first root. Both divide by means of septa inclined in different directions, and, it would seem, in a manner similar to that in which in the more advanced plant, the multiplication of the cells of the first degree takes place. I recognised the triangular form, when seen from above, of the apical cell of the principal shoot in *Aspidium filix-mas*, and the two edged form of the same cell, when viewed in a similar manner, of *Pteris aquilina*, after about three divisions had taken place in each of them. Even after the first round of divisions the stem-cell of the first degree ceases to multiply further: * a proportionally more rapid sequence of divisions begins in

* See the explanation to Pl. XXVIII, fig. 3 *b*, and Pl. XXVII, figs. 6 *b*, 7 *b*.

the cell of the second degree, contiguous to the mouth of the archegonium, which has been cut off from the stem-cell. This cell of the second degree is the primary cell of the frond.

That moiety of the primary cell of the principal shoot which adjoins the first cell of the primary abortive axis is considered to be a cell of the first degree, the principal reason for which is, that at a later period, and when the germ-plant is more developed, the cell in question appears as the apical cell of the stem. It would be a simpler mode of settling the rank of the cells, if that cell were considered to be of the first degree, in which the successive divisions take place, not only at the earliest period, but in the primary direction; and according to this method there would be no doubt that the primary cell of the stem, considered in relation to that of the frond, must be looked upon as a cell of the second degree; an opinion which might be made use of in support of the theory of the origin of the fern-stem from the amalgamation of the stalks of the fronds.* As, however, there are but few plants which exhibit so manifest a terminal bud (around and under which the appendicular organs take their rise), as the ferns do when they have attained some growth, it follows that here, as in the similar instances of monocotyledonous embryos, it is necessary in forming an opinion as to the rank of the cells, to have regard to the condition of the plant at a period subsequent to the formation of the cells in question.

In the two species immediately under consideration, the cell-succession in the first frond agrees substantially with that in the later ones, but at the same time it differs considerably. The surface of the first frond is, however, in its inception, parallel to that of the prothallium, as is the case in all the Polypodiaceæ which have been hitherto observed. The primary cell of the root divides in the first instance by septa turned towards the neighbouring cells; the division takes place twice by means of opposite septa (concave

* Considerations of this nature may have led Nägeli to deny that ferns have leafy stems ('Zeitschrift für wiss. Botanik,' Heft 3 and 4, p. 148); Hanstein's notion of the fern-stem also rests upon this foundation ('Linnæa,' 1848).

to one another in *Pteris aquilina*), so that the cell retains its original two-edged form; and three times by means of flat septa diverging from one another at angles of 60°, so that the cell assumes the shape of a three-sided pyramid with an arched under surface (Pl. XXVI, fig. 6). In both cases a septum is now formed parallel to the chord of the outer arc (Pl. XXVIII, fig. 1; Pl. XXVI, fig. 7). The flat cell cut off by this latter septum is the first rudiment of the root-cap, whose outermost, hood-shaped, cellular layer is formed by the multiplication of this cell. Henceforth the root-cell of the first degree lies surrounded by cellular tissue. Its further increase arises from repeated divisions occurring in the same succession.

Judging from its position, the first root of the young fern is adventitious, differing in no respect from the later adventitious roots of the full-grown plant. This view of the nature of the first root of the vascular cryptogams in general (a view which I expressed many years since*), has lately been objected to by Wigand. His first objection (an unfounded one) rests principally upon a conjecture that the foot-shaped portion of the germ-plant, that which I have called the primary axis, not only amalgamates with the prothallium, but is *probably* prolonged backwards so as to form the root. Wigand adds, "I consider that the enlargement of the lower part of the germ-plant is of a different nature; I look upon it as the undoubted rudiment of the first main root; it does not break through after the manner of an adventitious root." A few words of explanation are requisite as to the distinction between main roots and adventitious roots in general. Our conceptions of main roots rest entirely upon the observation, that the portion of the embryo of dicotyledons, which is situated beneath the cotyledons (and in most instances that portion of the plant alone) is prolonged downwards and becomes the root, and that in a normal state no portion of the plant above the cotyledons sends forth roots. Now, strictly speaking, the root by no means commences close underneath the insertion of the cotyledons, for between the latter point and the root there is to be

* Berlin 'Botanische Zeitung,' 1849, 797.

found the small embryo-stem which Irmisch calls the hypocotyledonary axis, and which Clos calls the *collet*. The place of origin of the root, *i. e.*, the lower end of the embryo-stem, is difficult to discover by direct observation, but may safely be defined as the point at which in the lower end of the very young embryo the cell-multiplication peculiar to the root commences. Now, whether the young root of the germinating plant has the appearance of an immediate prolongation downwards of the embryo-stem (as is the case with most dicotyledons, and with a few monocotyledons, such as Juncus, Allium, and Paris)—or whether it (the young root) breaks out from the interior of the lower end of the embryo, as in the Palms and the Loranthacæ—depends simply upon the fact whether the place of origin, the focus of cell-formation of the root, lies nearer to or further from the lower end of the embryo. In both cases the root is a main root. An adventitious root differs only in the fact, that its longitudinal axis does not coincide with the prolongation of that of the embryo, but forms with the latter a considerable angle. For instance, the Orchideæ, the Fluviales, and especially (as Irmisch has well observed), the Grasses, have no radicle, but only adventitious roots. The distance from the surface of the place of origin of adventitious roots is variable, being less in some plants than in others. In the former case the surface of the adventitious roots passes gradually into the cortical layer of that portion of the plant from which they spring, as may be observed in the pea when germinating. In the latter the adventitious roots pierce through the outer cellular cortical layers, throwing back those layers in the form of a ring round the place of egress of the roots. The absence of these characteristic collars (Coleorhizæ), at the base of the adventitious roots, is by no means unusual.* Ferns with creeping stems almost always have them, and those with upright stems not unfrequently. It is well known that all ramifications of roots, both those from main roots and those from adventitious roots, are formed from the outer surface of vascular bundles, and must therefore, without exception, break through the bark. The reason why

* See Irmisch's observations on 'Neottia nidus avis.'

no Coleorhizæ are usually visible here, is, that (as in the case of axile superficial adventitious-root-formation) the direction of the root-branch in its earliest stage, generally follows the axis of the root. The bark of the latter is pierced by the former during the young state of the cells before they have attained their final thickness. The continual amalgamation of the contiguous cells of the root and its branch obliterates all traces of the gradual perforation.

During the first divisions of the rudimentary cells of the stem, frond, and root, the two others of the four primary cells of the embryo multiply by the formation of oblique longitudinal and transverse septa (Pl. XXVIII, fig. 3; Pl, XXVI, fig. 6), so that the embryo assumes altogether a spherical form. Only the rudiment of the first frond appears at an early period as an elongated point.

From the time when the outer limits of the rudimentary cell of the root are fixed by the formation of the first cell of the root-cap, the cells of the upper surface of the primary axis, and also the neighbouring cells of the growing root, enter into close combination with the adjoining cells of the prothallium.* The result is a complete amalgamation of the adjoining outer surfaces of the cells, which cannot now be detached from one another by mere mechanical means. Henceforth the embryo which up to this point lay free in the cavity of the enlarged central cell of the archegonium, adheres firmly to the prothallium. The adjoining cells of each remain tolerably even. The attachment of the embryo is not the result of arrangements such as we find in the analogous process of the ingrafting of the fruit of a moss into the axis of the mother-plant; nor is there any elongation of the basal cell of the fruit rudiment into a capillary tube, becoming curved where it penetrates the stem, as is the case in many Jungermanniæ; nor is there as in Anthoceros any development of processes from the cells of the broad, slightly convex, under surface of the young fruit. ' From the moment of the commencement of the amalgamation, the cells of the

* See Mohl in 'Wagner's Handwörterbuch der Physiol.,' vol. iv, p. 279.

embryo which attach themselves to the prothallium divide by the repeated formation of transverse septa into groups of almost tabular cells. By this means the way is prepared for the subsequent not inconsiderable longitudinal extension of the primary axis of the embryo which is the result of cell-expansion.

The action of concentrated sulphuric acid soon loosens the connexion between the prothallium and the embryo. If the latter is detached the outer surface of its primary axis appears to be surrounded by a gelatinous envelope with radial markings: this is the loosened adhesive matter by which the embryo and the prothallium were united. The outlines of the cells of the latter are most clearly marked upon it by a net-work of narrow band-like protuberances.

The growth of the embryo is accompanied by an active multiplication of the cells of the prothallium adjoining the impregnated archegonium. This multiplication, which is not confined to the cells immediately adjoining the central cell of the archegonium, gives rise to the formation of a considerable cellular protuberance, attached to the under side of the prothallium, and which encloses the embryo. The circumference of this excrescence is usually very considerable in *Pteris aquilina*. The increase in growth of this cellular tissue usually keeps pace so completely with that of the embryo, that the expanding cavity is always exactly filled up. The multiplication of the neighbouring cells of the prothallium is not however caused by the pressure of the growing embryo upon the side walls of the central cell of the archegonium: this is manifest from the fact of the occurrence of exceptional cases of imperfect growth of the embryo, as has been observed, not only in many vascular cryptogams, but even in mosses.* The embryo, probably in consequence of imperfect impregnation, only occupies a small portion of the enlarged cavity of the central cell of the archegonium, as has been observed by comparing two impregnated archegonia of the same prothallium in *Pteris aquilina* and in *Aspidium filix-mas* (Pl. XXVIII, fig. 2);

* By Gottsche in *Calypogeia Trichomanes*, 'N. A. A. L. C.,' and by myself in *Frullania dilatata* and *Targionia hypophylla*. 'Vergl. Unters,' p. 41.

the same thing also has been noticed in *Salvinia natans* and *Pilularia globulifera*.

The active longitudinal growth of the first frond and of the first root of the young fern produces a constantly increasing expansion of the surrounding tissue of the prothallium, until the latter is ultimately unable to keep pace with the increase in size of the young plant. The layer of tissue surrounding the latter underneath, is ruptured transversely, usually somewhat in front of the neck of the impregnated archegonium. The frond immediately curves upwards, and appears between the two flaps of the prothallium. Before this period it has formed the rudiments of its lamina, which in all ferns are much less divided in the young, than in the full-grown plant. The first fronds of *Polypodium vulgare*, for instance, are not unfrequently undivided and lanceolate-shaped; more often however they are divided at the apex into two portions of very unequal size. Contemporaneously with the appearance of the first frond, the first root also pierces downwards through the tissue of the prothallium. Immediately after it makes its appearance it turns downwards into the ground.*

If the second frond of the germ-plant is developed very soon after the first, the surrounding cellular tissue of the prothallium in the neighbourhood of, or above the point of egress of the first frond, is pushed outwards and forwards, and is ultimately broken through. Before the frond makes its appearance out of this covering, the latter resembles a conical wart protruding into the indentation of the fore edge of the prothallium: it is the body which Wigand ('Bot. Zeit.' 1849, p. 121) has described as the prolongation of the midrib of the prothallium.

* Von Mercklin asserts ('Beobacht. am Prothallium der Farrnkr.' Petersburg, 1850) that soon after the appearance of the embryo in the interior of the prothallium, a dark stripe becomes visible, passing from the base into the mass of the prothallium, and expanding itself there. It contains a bundle of shortly-jointed, striped vessels, the pointed ends of which reach to the neighbourhood of the archegonia. The older the prothallium the more numerous are these vessels, which, in their configuration, answer exactly to those of the large vascular bundles of the first frond, and appear never to be wanting. I find the prothallia of all the ferns which I have examined to be always composed of homogeneous parenchyma, and to be devoid of vessels. I have not the least notion what Von Mercklin's supposed striped vessels can be.

Development of the vegetative organs.—The similarity in the development of the different species of ferns does not extend beyond the formation of the rudiments of the first frond and of the first root.

So far as regards the mode of development of the vegetative organs, the two commonest ferns of Germany represent the terminal points of the long series of multifarious forms of the most extensive family of the vascular cryptogams. *Pteris aquilina* affords one of the most perfect examples of a fern with a creeping stem, having the fronds arranged in two lines, and with a most decided tendency to bifurcation of the terminal bud. The greater number of the ferns inhabiting the forests of the torrid zone comport themselves like *Pteris aquilina*. *Aspidium filix-mas*, on the other hand, forms a stem tending upwards, and agrees essentially in its habit, in the arrangement of its fronds, and in the division of its vascular bundles, with the tree-ferns of the tropics. The following observations will treat of the history of the development of the two ferns just mentioned, and we will proceed first with *Pteris aquilina*.

Pteris Aquilina, L.—The surfaces of the septa formed in the cell of the first degree in the first frond of *Pteris aquilina* are turned towards the apex of the stem.* A plane passing through the longitudinal axis of the stem and of the frond, is at right angles to the lateral surfaces of the wedge-shaped apical cells of both organs (Pl. XVIII, fig. 6). Even at a very early period, before the enveloping cellular layers of the prothallium are ruptured by the longitudinal growth of the first frond, septa are formed in the apical cell of the frond on the right and left of its median line. These septa are at right angles to the fore and hind walls, and they change the form of the cell, which has hitherto been wedge-shaped like a segment of an ellipsoid, into a three-sided prism with the edge turned downwards and having its hinder surface

* This is the case also with all the subsequent fronds not only of *Pteris aquilina* but also of other species of the same genus; as well as with the fronds of such ferns as *Pteris serrulata*, which have a triple frond-arrangement, and where the apical cell of the terminal bud has the form of a three-sided inverted pyramid. In the Polypodiums and Aspidiums the circumstances are widely different.

arched. The longitudinal growth of the frond is also forwarded by the production of septa which are parallel to the fore and hind walls of the cell of the first degree, and are turned towards the surfaces of the frond. From time to time, however, the apical cell divides anew by longitudinal septa at right angles to those just mentioned, and the end of the young frond is by this means widened. Thenceforward both forms of division continue to take place in the marginal cells of the frond which adjoin the apical cell; but the activity of division diminishes in a lateral direction, and terminates far above the place of insertion of the frond. That portion of the frond which is situated above the point at which the multiplication of the marginal cells terminates, becomes the blade of the frond, and the portion below that point becomes the stem of the frond. The cell-succession of the leafy portion of the frond therefore much resembles that of the flat stem of the Marchantieæ and Ricciеæ; but there is invariably one cell only of the first degree; not two.

The formation of the pinnæ of the frond in the species of Pteris, as in the rest of the Polypodiaceæ, is the result of a true bifurcation of the apical *punctum vegetationis*. This formation commences with the division of the apical cell by a septum coinciding with the median line of the frond, and perpendicular to its surfaces. Each daughter-cell is divided by a septum almost parallel to the longitudinal axis of the frond (Pl. XXIX, fig. 3). This latter division occurs either immediately, or after the previous formation of septa which are inclined to the surfaces of the frond, and contribute to its longitudinal growth. The three-sided cell on the right and on the left of each of the two pairs of cells which occupy the middle of the fore edge of the frond, becomes the seat of fresh cell-multiplication, and is the cell of the first degree of a pinna of the frond. Each of the new shoots is alternately more strongly developed, thus changing the direction of the bifurcation to the right or to the left. The weaker one is pushed on one side so as to appear to be lateral. The continual change in the direction of the less vigorous bifurcations causes the feather-like form of the frond, whose segments (as is well known) are in no species

exactly opposite to one another. The position of the first lateral bifurcation on the mid-rib is not constant in any species; in *Pteris aquilina* it is more often to the left, in *Aspidium filix-mas* to the right. The principal segments of the fronds, however, taken in relation to their subsequent ramifications, are very regularly antidromal: on the pinnæ to the left of the axis of the frond the first segment of the second degree, or the first tooth of the margin, is on the right: on the pinnæ to the right of the axis it is on the left.

From the first commencement of the frond its growth in thickness is most vigorous behind. Its mathematical longitudinal axis is not identical with the morphological one; it does not coincide with the surfaces of contact of the masses of cells, produced by the multiplication of the cells of the second degree, which are turned towards the front and back surfaces of the frond. At the time of the commencement of the formation of the blade of the frond, which is produced by the widening of its apex, the cell-multiplication in a longitudinal direction increases on the hinder surface of the frond. It exceeds that which takes place on the front surface and thus leads to the commencement of the rolling inwards of the frond (Pl. XXIX, fig. 1), which is completed by the stretching of the cells of the hinder surface which shortly afterwards takes place. Contemporaneously with the commencement of the rolling inwards, the axile longitudinal rows of cells separate themselves by the cessation of transverse division, and become transformed into the simple vascular bundle which traverses the stem and mid-rib of the frond. Four cells of the adjoining parenchyma are about equal in length to one of the cells of the rudimentary vascular bundle. This latter passes through the morphological longitudinal axis of the young frond, near its front surface. It is concave in a transverse section, open towards the front (Pl. XXIX, fig. 14).

During this development of the frond, the first root also has grown considerably. Its axile rudimentary vascular bundle becomes visible contemporaneously with that of the frond. The two meeting together in their entire breadth

underneath the terminal bud,—which in the mean time has become developed into a cellular wing,—form a connected, slightly curved, string of cambium, upon which the wing is attached sideways (Pl. XXIX, fig. 1).

Now whilst the cellular layers surrounding the embryo are ruptured by the longitudinal growth of the frond and root, the cells of the primary axis also become considerably elongated, so that the germ-plant is removed from the prothallium as if borne upon a short stem; an appearance which brings to mind the normal process in Salvinia. The innermost cells of the primary axis adjoining the vascular bundles of the frond and of the root assume a prosenchymatal form (Pl. XXIX, fig. 1), and at a later period become woody scalariform cells, so that the ligneous body of the germ-plant has a blind-ended short prolongation reaching into the primary axis.

The growth of the stem-bud, which is rapid in comparison with what occurs in other ferns, and which is observable whilst the embryo is yet enclosed (Pl. XXVIII, figs. 4, 5), increases still more after the latter has emerged from the prothallium; the end of the stem becomes a somewhat slender cone (Pl. XXIX, fig. 1). The formation of the second frond commences even before any thickenings of the membrane make their appearance in any of the cells of the rudimentary vascular bundles of the germ-plant. The second frond originates in the multiplication of a cell of the apex of the stem situated on that side of it which is turned away from the point of attachment of the first frond, and distant from the latter by about half the circumference of the stem. The cell-multiplication of the second, and of all the subsequent fronds, follows the same rule as that of the first: it begins by the continually repeated division of the cell of the first degree, by means of septa inclined alternately towards and away from the top point of the stem. After the rudiments of the stipes of the frond are fully formed, the apical cell divides by longitudinal septa at right angles to the fore and hind surfaces; in all the cells of the thus expanded fore-edge, division occurs by septa inclined alternately towards the upper and under surfaces of the frond.

Almost contemporaneously with the appearance of the second frond, numerous cellular hairs are seen upon the terminal bud of the stem, which have been previously visible, although more sparingly, upon the first frond. Having regard to their position and their centripetal development, they are undoubtedly analogous to the scales of other ferns, which indeed also appear primarily elsewhere under the form of simple rows of cells.* In *Pteris aquilina*, *Dicksonia rubiginosa*, and *Balantium Karstenianum* they do not progress beyond this primary stage of development.

From the time of the formation of the second frond until the commencement of that of the third, the longitudinal growth of the axis increases considerably, as it does with each successive frond during the entire life of the plant, unless prevented by unfavorable influences. At this time, if not (as is not unfrequently the case, Pl. XXIX, fig. 1) even before the formation of the second frond, a twisting of the stem takes place. If the young stem is supposed to be horizontal, the hinder surface of the first frond is turned downwards; the rudimentary frond was parallel to the surface of the prothallium.† By the torsion of the axis the direction of the third frond, and sometimes even of the second, is turned away from it to the extent of 90°. Henceforth the fronds are inserted on the sides of the creeping stem, the fraction $\frac{1}{2}$ representing as before their mode of arrangement. The plane of involution of the budding stem (that plane in which all the turns of the incurved leafy surface lie, and which is perpendicular to the leafy portion of the frond) is at first radial to the axis of the latter. This plane, however, soon stands at right

* I will return to this subject hereafter. Multicellular hairs with intercalary cell-multiplication, even in the direction of the breadth and thickness, occurs here and there even on the leaves of phænogams (*e. g.* Begonia, and the calyx and corolla of *Hibiscus Trionum*). My observations do not confirm Kunze's opinion that the shoots at the base of the stipes of *Hemitelia capensis*, which resemble the fronds of Trichomanes, are transformed scales. The reasons therefore which induced me to consider the scales as leaves, and the fronds consequently as leafy branches, fall to the ground. The scales are only a kind of hairy covering; certainly a very highly developed one, as they frequently contain chlorophyll; for instance in Platycerium.

† It is self-evident that in speaking thus of the direction of the frond no account is taken of the secondary curving upwards of the stipes to the light.

angles to the axis, on account of the rapid horizontal longitudinal growth of the stem, which far outstrips the development of the frond; and the result is that the surfaces of the frond are parallel to the axis. The stalks even of the first fronds exhibit the appearance* which occurs in the stipes of almost all fronds, that is to say, prominent bands of loose cellular tissue having the intercellular cavities filled with air pass along the side edges of the stipes; which bands are in connexion with, and of the same nature as, the inner parenchyma, which latter, except where it is traversed by the bands, is enclosed by a firm cortical tissue (Pl. XXX, figs. 7, 9). The creeping stem of *Pteris aquilina* (Pl. XXX, fig. 3), and the stems of the exotic Dicksoniæ, which are similar in their habit, exhibit the same quality. The lateral ridges of the stem pass directly into those of the fronds (Pl. XXIX, fig. 14).

At an early period the germ-plant exhibits that premature vigorous development of the peripheral cellular layers of the stem in the immediate neighbourhood of its terminal bud, which afterwards has a marked effect upon the form and position of the apex of the stem. The growth in thickness of the cortical tissue of the next younger portion of the stem is very rapid, and by the time that the third frond is developed, the apex of the stem appears to be sunk in that tissue (Pl. XXIX, fig. 6).

The internal structure of the young stem, like that of the first frond, is very simple. From the point of junction of the vascular bundles of the first frond and first root there is developed a central vascular bundle, traversing the young stem (Pl. XXIX, figs. 5, 6, 7), from which the transformation into vascular bundles of the strings of cellular tissue which pass into the newly-formed fronds commences, and on the outer surface of which the development of new adventitious roots begins (Pl. XXIX, fig. 6). The direction of the second and of the next following root diverges by about 90° from a plane passing through the first frond and the longitudinal axis of the stem (Pl. XXIX, fig, 6). The subsequent roots exhibit no trace of this regular arrangement.

After the formation of from seven to nine fronds, the

* Karsten, 'Vegetations-organe der Palmen,' p. 129.

stem becomes forked by the division of its punctum vegetationis. Each branch of the fork increases rapidly and considerably, and about equally, in thickness. The first frond of each is usually situated to the right hand (Pl. XXIX, figs. 10, 11). From this time forth the course of the vascular bundles of the stem is a compound one. The lateral opening of the central vascular bundle becomes enlarged (Pl. XXIX, fig. 8). Its upper half is soon separated from the lower; the vascular bundle is prolonged, whilst the tissue of the bud of the stem remains parenchymatal. The stem has now two flat vascular bundles (Pl. XXIX, fig. 9) parallel to the axis, which here and there split into thinner forked branches which soon unite again (Pl. XXIX, fig. 9^b). When the furcate shoots have attained a length of about three inches, and their transverse diameter is about two lines wide, the two large vascular bundles send out less vigorous bundles which take a direction nearer to the bark, and of which the uppermost one, which passes above the axile bundles, is somewhat more fully developed, and is about equal in breadth to the latter (Pl. XXIX, figs. 12, 13). The cortical vascular bundles anastomose in the vicinity of the place of insertion of each frond, and thus form a hollow cylindrical network of elongated meshes. But no connecting branches between them and the axile bundles are to be found anywhere in the stem. The latter follow an entirely isolated course within the creeping stems; ramifications from them enter the fronds, and it is only these ramifications which are met inside the stipes by ramifications from the cortical vascular bundles. Roots originate only from the latter bundles.

The stems of fully grown plants exhibit, in all essential points, the same distribution of vascular bundles. The number of the peripheral ones amounts to as many as twelve. The two uppermost of the latter are blended together for the greater part of their course, and thus form a wide bundle, which lies in the same vertical plane as the primary axile bundles. Two masses of cells almost parallel to these primary vascular bundles, and situated between them and the peripheral vascular bundles, become

very woody, like bast-cells. Their very thick walls, which are pierced by pits or canals, assume a brown colour throughout. Thin sections of them are of a beautiful golden yellow; when seen in a mass they are almost black. The axile region of the stem thus appears, even to the naked eye, to be distinctly separated from the bark by a thick hard sheath of vascular bundles, which has a fissure-like longitudinal opening only on each of the two sides parallel to the outer longitudinal bands of the stem (Pl. XXX, fig. 3). One of these fissures is often closed by an amalgamation on one side of the two halves of the sheath of vascular bundles. The upper half of the sheath is tolerably flat; the lower one has the form of a furrow. During the transformation of the parenchymatal cells of the end of the stem into bast-cells, air-bubbles are formed (Pl. XXX, fig. 12), between the walls of the latter, in the interior of small irregularly-defined intercellular cavities. These air-bubbles disappear when the thickening of the walls commences.

The outermost cellular layers of the bark also assume a deep brown colour, but without becoming prosenchymatous, and without any material thickening of their walls. Those portions only of the tissue which pass towards the lateral longitudinal ridges do not assume this brown colour, which extends to the depth of one-eighth of a line into the cortical tissue. The portions just mentioned, like the parenchyma of the interior of the stem, remain of a dazzling white: they contain starch, and their intercellular cavities are filled with air. Here and there in this tissue, and sometimes also in the brown-coloured outer cortical layer spindle-shaped groups of combined cells become transformed into thick-walled bast-cells, similar in all respects to those of the sheath of vascular bundles.*

As the vascular bundles in the growing stem become more complicated, so also do those in the stipes of the fronds. As in the first, so also in the other fronds of the young plant up to the twelfth, the vascular bundles unite to-

* Mohl objects to these cells being called bast-cells ('Vermischte Schriften,' p. 116), but in their form and mode of development they agree exactly with the bast-cells of phænogams.

gether to form a single one. The transverse section of this single bundle has the shape of a horse-shoe, of which the opening is originally turned towards the apex of the stem-bud, but which in consequence of the rapid longitudinal development of the latter, and of the curving upwards of the frond, appears at a later period to be parallel to the longitudinal axis of the stem. After the splitting of the primary vascular bundle, and the appearance of cortical vascular bundles in the stem, there arise ramifications of both the axile bundles, of the wide bundle above them, and of the rest of the cortical vascular bundles of the adjacent longitudinal half of the stem (Pl. XXX, figs. 1^a to 1^e, and fig. 2). The sheath of vascular bundles also sends out prolongations into the stipes: from the upper as well as from the lower group of brown bast-cells the same transformation of the tissue advances in a direction parallel to the longitudinal axis of the frond (Pl. XXX, fig. 7). At a short distance above the place of insertion of the frond, both longitudinal strings of ligneous tissue unite to form a single one of which a transverse section exhibits the shape of the letter T having the two branches of its head turned to the lateral longitudinal ridges of the frond (Pl. XXX, figs. 8, 9). The hind angle of the T includes the ramifications of the two axile primary bundles of the stem; the fore angles those of the wide cortical vascular bundle which runs off in the top line of the horizontal stem, as well as the branches of the cylindrical cortical vascular bundle immediately adjoining. In front and on the outside of the head of the T, run the bundles which sent forth the cortical bundles underneath the place of insertion of the frond. In the lowest part of the stipes, underneath the point of junction of the prolongations of the vascular sheath, all these vascular bundles anastomose in a radial direction; above this point only in a tangential direction. Each of the primary vascular bundles sends two proportionally thin cylindrical branches into the frond (Pl. XXX, figs. $2^{d,e}$). All four soon unite to form a wide vascular bundle concave behind (Pl. XXX, figs. 8, 9). A similar bundle is formed by the junction of those bundles which are enclosed by the fore angle of the T-shaped mass

of brown cells. It is this distribution of the tissue composing the stipes which produces the well known figure of the eagle seen on an oblique section.

Delicate longitudinal sections through the terminal bud of the stem of *Pteris aquilina,* exhibit with the greatest clearness the transformation of the originally homogeneous parenchymatal tissue into vessels and bast-cells. The investigation is very much facilitated by the course of the inner one of the two primary vascular bundles, which is straight and parallel to the axis. According as the section is taken parallel to the surface of the earth, through the longitudinal ridges of the creeping stem, or at right angles to this direction, the wedge-shaped cell which encloses the apex of the flatly conical deeply buried terminal bud is seen either on its three-sided front aspect (Pl. XXXI, fig. 5), or its four-sided lateral aspect (Pl. XXXI, fig. 4). The funnel-shaped depression, at the bottom of which the terminal bud is seated, is strongly compressed from above and below. The walls of the depression are thickly clothed with scale-like hairs. The erect ends of the hairs, which are closely pressed against one another, and fastened together by a hardened mucilage secreted from the bud, entirely close the mouth of the funnel, and shut off the delicate young portions at its base from the outer air. The end of the stem in its longitudinal growth forces its way through the toughest clay, without injury to the delicate bud buried in its apex.

The clearly defined mode of arrangement of the cells of the second degree, and of their derivatives, affords an immediate explanation of the deep depression of the terminal bud. The cell of the first degree is wedge-shaped (Pl. XXXI, figs. 2—5), as is manifest by comparing its apical, front, and side aspects. It is bounded by three curved surfaces, the upper free wall of the cell representing a portion of a spherical surface enclosed by two flattened arcs, and the side-walls being two segments of a conical surface. The septa which arise in the cell, and which are alternately parallel to the one and the other of the simple curved lateral surfaces, form cells of the second degree, having the shape of the fifth part of an oblique hollow

cone. These divide successively by means of longitudinal septa which are parallel to each one of their small lateral surfaces, and diverge strongly from the radii of the stem, into from three to five cells, adjoining the cell of the first degree (Pl. XXXI, fig. 3 *b*); a form of multiplication in which variations sometimes occur by which the next step in the development is anticipated (Pl. XXXI, fig. 2). The newly-formed cells then divide gradually by means of septa parallel to the lateral surface of the apical cell into twos; those cells which are situated anteriorly to the middle of the sides of the apical cell dividing sooner than those adjoining the lateral corners. The cells thus formed, whose increase in height and in width (*i. e.*, parallel to the lateral surface of the apical cell) far exceeds their increase in thickness, divide by means of transverse septa into low, almost cubical, inner cells, and elongated outer cells, with a free outer wall (Pl. XXXI, figs. 4, 5). The expansion and multiplication of the cells of each of the groups derived from a cell of the second degree, preponderate considerably in the lower portion and in a transverse direction; and the same thing occurs in the cells derived from the youngest of the four cells of the second degree, whose free outer walls compose the conical interior portion of the stem-bud (Pl. XXXI, figs. 4, 5). In the longitudinal section of the stem the boundary lines which enclose each such group of cells exhibit strongly protruding angles on the side turned away from the apex of the stem: the side walls of the cells composing the outer surface of the stem-bud, are inclined inwards towards their summits. In the next older group of cells the direction of the suddenly-augmented cell-multiplication is reversed. Here the cells of the circumference often divide repeatedly by means of septa parallel to the chord of the arc of the outer wall, and perpendicular to the side-walls. This is a growth in thickness, an increase of the cortical tissue in a direction at right angles to the axis, but in consequence of the unusual direction of the cells in which it occurs, it takes place at first apparently in an upward direction. The bud becomes surrounded by a high, narrow, annular wall. The growth of the latter is particularly active in the direction of a plane cutting the

lateral bands of the stem at right angles; here the internal septa of the annular wall become perpendicular, or even overhanging. Its cells appear arranged in concentrical scaly layers round the middle point of the stem-bud.

During the formation of the annular wall the activity of cell-multiplication in the longitudinal direction (*i. e.*, in the direction of lines drawn in a radiating manner from the apex of the stem-bud along its sides) increases, and obliterates the arrangement of the cells visible in the apical aspect of the youngest portions of the bud, viz., the system of flattened arcs surrounding the middle point of the stem. In its place the arrangement in (apparently radial) longitudinal rows becomes more manifest; this is produced by the repeated division of the cells by means of septa at right angles to the outer surface, and perpendicular to the radial planes passing through the axis of the stem.

The prolongation of the two primary axile vascular bundles begins to be differentiated from the rest of the tissue at a very little distance beneath the terminal bud, and in or near the mass of cells derived from the eighth-youngest cell of the second degree. The separation of the peripheral vascular bundle commences somewhat further from the apex of the stem. Both phenomena arise from the fact, that in the strings of cells which are transformed into vascular bundles, the transverse division which continues to take place in the neighbouring tissue, diminishes and ceases, whilst the division by means of longitudinal septa is hastened. The rudimentary vascular bundles appear therefore as streaks of narrow elongated cells, whilst in the cells of the remaining tissue no one of the three dimensions preponderates to any great extent (Pl. XXXI, figs. 4, 5). Certain cells of the vascular bundles arranged in longitudinal rows, become widened at a very early period. Afterwards they are transformed into the scalariform cells which form the principal mass of the perfect vascular bundle. In the first instance they are placed one upon another, and furnished with horizontal transverse septa: they assume their permanent spindle shape even before the first traces of thickening layers are visible upon their inner walls (Pl. XXX, fig. 12; Pl. XXXI, fig. 1). The first appearance

of the thickenings of the wall is in the form of delicate transverse streaks, and commences long before the termination of the longitudinal growth of the cell, and even during the existence of the parietal nucleus and of the strings of granular mucilage proceeding from it (Pl. XXXI, fig. 1).

Long before the appearance of the first traces of the thickenings of the walls of the scalariform vessels, spiral thickenings are visible in certain cells arranged in groups of twos or threes and which at an early period become spindle-shaped. It is very clearly seen that the formation of the spiral band proceeds gradually from the lower to the upper end of the cell (Pl. XXX, fig. 12). In each vascular bundle these small groups of spiral vessels are formed: one axile group is formed in those vessels which are circular in a transverse section, and three are usually formed in those bundles whose transverse section is elongated; one of such groups being in the centre, and the others in the foci of the figure presented by the transverse section, and which bears a distant resemblance to an ellipse.

The great expansion of the cells of the vascular bundle which go to form the scalariform vessels, causes such a compression of the intermediate, narrow, prosenchymatal cells, that in some instances the entire cavity of the latter is obliterated.

A transverse section of the youngest portion of a vascular bundle taken at a point near the terminal bud where the thickening layers are visible only in the spiral vessels, exhibits a considerably larger number of cells than is seen in the same vascular bundle at a distance of about a line and a half from the terminal bud after its scalariform vessels are completed (Pl. XXX, figs. 10, 10^b). A similar state of things exists in the vascular bundles of the stipes. Transverse sections of the compressed cells, provided the cavities of the latter are not quite obliterated, bear a considerable resemblance to the lenticular cavities between two pits of coniferous wood (Pl. XXX, fig. 2, *between the two wide vessels*).

The course of the vascular bundle nearest to the middle of the stem (*i. e.* of the upper one of the two primary ones), is almost exactly parallel to the longitudinal axis close

under the bud of the stem. But in consequence of the subsequent growth in length and thickness of the interior of the stem, the other axile bundle, and still more the cortical bundles, are bent strongly inwards towards the longitudinal axis of the stem as long as their course passes within the prematurely developed peripheral tissue. This bending usually amounts to 99° in the cortical bundles (Pl. XXX, fig. 4; Pl. XXXI, fig. 1). A transverse section passing through, or just over, the apex of the bud, exhibits the vascular bundles which run almost horizontally to the apex, in the form of from six to eight light streaks united in a stellate manner.

Soon after the appearance of thickening layers in those cells of the axile bundles which have become widened into scalariform vessels, there ensues such a considerable growth of the cells of the interior of the stem, that the disproportion of the latter to the peripheral cellular layers disappears. The bent portion of the cortical vascular bundles takes a straight course; the height of the axile cells becomes almost equal to that of the cortical cells of the same age; which latter cells had far outstripped the former in development, especially in the thickening of the cell-membrane, as is perceptible in the peripheral vascular bundles. As the growth of the interior of the stem (by means of the extension of its cells) surpasses that of the bark, which was prematurely developed by more vigorous cell-multiplication, the cells of the interior are three or four times longer than the peripheral cells. The process may be considered as a pushing outwards of the funnel-shaped depression around the terminal bud. It occurs in like manner in Isoetes, Cycas, Mamillaria and elsewhere, but much less distinctly on account of the close crowding together, of the appendicular organs.

The formation of new fronds always takes place above the point of origin of the youngest scales. At some distance from the top cell of the apex of the stem, and separated from the latter by from three to six cells, the mother-cell of the frond is first visible in the form of a slight elevation above the flat conical surface of the bud (Pl. XXXI, fig. 3). The first step in the formation of a frond however

very probably consists in the occurrence from time to time of the division of a newly formed cell of the second degree by means of a slightly convex longitudinal septum, turned towards the cell of the first degree, which cuts off from the cell of the second degree a daughter-cell, whose form coincides with that of the apical cell of the stem (Pl. XXX, fig. 2). The rudiment of the frond bears considerable resemblance to the end of the stem in the arrangement of its cells, but is distinguishable by the greater curvature of its arcuate surface, and by the very early appearance, (although at first in small quantity), of chlorophyll in its cells. The growth of the frond in length and thickness is at first very slow. The rapidly elongating apex of the stem soon leaves it behind. Whilst the premature development of its cortical tissue commences on the side turned to the young frond, the wall-like elevation of the circumference of the stem in the neighbourhood of the terminal bud pushes itself at an early period into the space between the two. The frond and the end of the stem which at the first appearance of the former are enclosed in the same depression of the bark, are now each of them situated at the base of a special funnel-shaped depression. The tips of the scales which clothe their walls protrude above each depression in a penicillate manner (Pl. XXX, fig. 5).

Whilst the germ-plant in the first year produces as many as twelve slender fronds whose development is continually progressive, the development of the fronds of older plants, which is frequently interrupted by long periods of cessation, requires several years. It is a rule, departed from only in cases of sudden alteration of the conditions of vegetation, (such as the ploughing up of the ground of a wood), that each shoot of the mature plant sends out yearly only one frond.* New fronds are produced towards the end of the vegetative period which lasts from April till October. In the first year the frond assumes no greater development than that of a low, laterally flattened, green wart of cellular tissue, situated at the base of a depression of the bark of the stem, distant at the most not more than a line from the apex of the stem. In the following year

* See A. Braun, 'Verjüngung,' p. 63.

(until the end of May) the stem rapidly elongates to the extent of about an inch, and during this period the portion of the stipes of the young frond which afterwards assumes a brown colour, is formed: it is a cylindrical body, one or two inches high, having a vertical direction produced by violent curvature close to its place of insertion, and clothed with yellowish-white scales (Pl. XXIX, fig. 14). After the removal of the latter a flat furrow is visible at the apex of the young frond on the side turned towards the stem, in which the rudiments of the lamina of the frond are closely folded in the form of a flat cellular mass, about one eighth of a line long, exhibiting two or three furcate ramifications (Pl. XXX, fig. 6, 6 *b*). Towards the end of the second vegetative period this cellular mass attains the length of one line, and makes from ten to twelve furcations, alternating to the right and to the left hand. The further development of the frond goes on in the spring of the third year, at the end of May in which year it appears above the surface of the earth, delicately rolled up like a crosier, and complete in all its parts.

Roots are developed only from the cortical vascular bundles of the stem of mature plants, and in fact only from the points of junction of their meshes. Their rudiments are formed close under the terminal bud, at the point where the course of the cortical vascular bundle exhibits its inward curvature (Pl. XXXII, fig. 1). Here cell-multiplication commences in one of the outer cells of the cambium bundle, similar to that by which the first root of the germ-plant is formed. As in that case, the three different kinds of septa of the cell of the first degree stand at right angles to a radial plane passing through the longitudinal axis of the stem. A septum is formed turned towards the vascular bundle from which the root is developed, and making an angle of about 30° with the root. This septum has the form of the third part of the surface of a truncate cone, and its formation is followed by that of a curved septum inclined in an opposite direction, this again is followed by the formation of an almost flat transverse septum at right angles to the longitudinal axis of the root, and diverging from the two former by about 60°. The form of the pri-

mary cell of the root agrees with that of the apical cell of the stem, except that the side-walls of the former are more strongly curved (Pl. XXXI, fig. 6 *b*; Pl. XXXII, fig. 1 *b*). The layers of the root-cap, which on account of the more vigorous growth at their median point are convex outwards, are developed from the cells of the second degree, which latter are formed by the production of flat septa parallel to the basal surface of the primary cell. The permanent main portion of the root is produced by the continual division of those cells which have the form of the third part of a hollow cone. The latter cells are first arranged in paraboloidal layers, which in the one longitudinal moiety of the root protrude for about half the length of a cell beyond the layers of the other moiety of the root. In the cells derived from the third oldest cell of the second degree, this symmetrical arrangement is changed into a homogeneous one, whilst transverse septa parallel to the primary septa appear in all the cells of the layer (Pl. XXXII, fig. 1 *b*). The mode of differentiation and formation of the axile vascular bundle, and the delay which at first occurs in its longitudinal development compared with that of the bark (a delay which is afterwards compensated by expansion), are common to both the root and the stem.

Ramifications of the root spring from its vascular bundles in the same manner as the roots spring from the cortical vascular bundles of the stem. The roots of the second degree, as well as their ramifications, which are not of frequent occurrrence, are arranged in two lines.

The greater the age attained by a shoot of the Eagle Fern—whether such shoot proceed directly from a prothallium, or from a bud, or whether it be the single branch of a forked stem—the greater is the tendency to furcation of its terminal bud. Ultimately, in really old individuals, frond-formation ceases entirely on the furcate branch when more strongly developed. Only the more delicate forked shoots which are placed alternately to the right and to the left bring forth fronds; the first one being always in the inner angle. The naked unbranched terminal shoots of those plants whose sympodium (which has the appearance of a principal axis) bears no fronds, is developed with ex-

treme rapidity, and produces an abundance of roots. Unbranched terminal shoots of this kind, of from six to ten inches long, are not rare. In these shoots the lower part of the annular wall which surrounds the terminal bud, protrudes itself forward in a labiate form, so that it eventually lies upon the upper surface of the gradually flattened shoot (Pl. XXX, fig. 4). The distribution of the vascular bundles in these unbranched, frond-less ends of shoots, exactly corresponds with that of the frond-bearing stem; a convincing proof that the arrangement of the vascular bundles in the stem is not dependent upon the position of the appendicular organs, or the number and form of the bundles occurring in such organs.*

The two wide axile vascular bundles are entirely devoid of branches in each joint of the sympodium. At each fork they send out into the more delicate shoot vigorous branches which constitute the axile vascular bundles of the latter shoot. I have met with sympodia four feet long devoid of fronds. The distances between two furcations are very unequal, and manifestly dependent upon the amount of nourishment being greater or less. The entire ramification of the plant, so far as it depends upon the furcations of the terminal buds, and the position of the fronds on these ramifications, correspond entirely with the pinnations of the blade of the frond. These latter are only distinguishable in their first rudiments from the furcations of the terminal bud, by the upward direction of the growth of the frond: they do not differ in their cell-succession.

Buds from which new shoots may be, and are developed, are found in *Pteris aquilina* only on the under side of the stipes; sometimes low down, sometimes higher up. Sometimes they appear so early and are so near the place of insertion of the frond that at first sight they appear to belong

* The same conclusion may be drawn from the condition (observed by H.-v. Mohl, 'Verm. Schriften,' p. 111,) of the upper ends of the vascular bundles of all ferns, especially of those with creeping stems and bilinear phyllotaxis (see Pl. XXXV, fig. 4): although the relations in question do not elsewhere stand out in so marked a manner. The conclusion given above would be valid even if the objections raised by Mettenius against my views of the mode of ramification of *Pteris aquilina* ('Abhandl. K. Sächs Ges. der Wiss.,' b. vii, p. 621,) could be maintained, which, however, as I shall hereafter show, is not the case.

to the stem. They originate from the multiplication of one of the cells of the free outer surface of the very young frond, and are situated on its back or at the edges,* they occur long before the first rudiment of the vascular bundles separates itself from the rest of the tissue (Pl. XXXII, fig. 2). The divisions of the primary cell of the new shoot follow the same rule as those of the apical cell of the mother-axis. When the development of the bud goes on slowly, the cortical tissue closes almost entirely over it (Pl. XXXII, fig. 3). An accurate observer however may even then discover the passage leading to the punctum vegetationis, which is merely stopped up by entangled and agglutinated scales (Pl. XXXII, fig. 3′): the passage is blocked up by the drying of a portion of the mucilage, which these buds of *Pteris aquilina* secrete in abundance.

Aspidium filix-mas.—The rudimentary and apical cells of the first, and of all the succeeding fronds of this fern, divide by means of septa inclined to the edges of the frond alternately to the right and to the left; the line in which each new septum cuts the next older one, is radial to the axis of the stem. As far as can be gathered from the result of numerous observations, the first septum which appears in the cell of the first degree, is inclined to the left,† and turned towards the next older frond (Pl. XXVI, fig. 14). This form of division continues until the completion of the rudiment of the stipes. When the formation of the blade of the frond commences, septa make their appearance in the cell of the first degree, and in the cell next to it of the second degree, which septa are inclined alternately towards the front and the hind surface of the frond. Thus the arrangement of the cells in the growing portions of the frond is coincident

* Upon the supposition of the adventitious bud being produced by the multiplication of a cell in the interior of the tissue, for instance, a cambial cell of a vascular bundle, the gemmæ of ferns would not be adventitious buds. But this definition is too narrow, and could not be employed in many of the instances which occur in phænogams.

† Following Braun's rule ('N. A. A. C. L.,' xv, p. 220,) of using the expressions *right* and *left* with reference to the direction of the development of the organic body in question, I call that margin of the frond the *right* margin which would be on the right hand of the observer, supposing him to be placed in the longitudinal axis of the frond, with his face to the upper surface. This margin of the frond is the front margin, turned towards the ascending leaf-spiral.

with that above described in *Pteris aquilina*, and the mode of ramification of the blade of the frond is the same as in the latter plant (Pl. XXVI, fig. 8).

The germ plant of *Aspidium filix-mas* developes its second frond at a distance of about a third of the circumference of the stem from the first. At the point of junction of the vascular bundles of the first frond and of the first root, there is formed a vascular bundle, which, after traversing the axis for a short distance, bends off into the second frond (Pl. XXVI, fig. 13). The second root is developed from that part of the vascular bundle which is situated in the stem, and at some little distance beneath the place of insertion of the second frond. The third frond diverges from the second, and the fourth again from the third, at about 120° to the right, so that the fourth stands vertically over the first. At the bending-point of the vascular bundle which passes out of the longitudinal axis of the stem into the second and succeeding fronds, there is produced a vascular bundle, which, after passing along the axis of the stem for a short distance, bends off into the next younger frond. Transverse sections of the stem exhibit only one vascular bundle (Pl. XXVI, fig. 12). The length of the stem between each two of the first four, five, or six fronds, is much greater than between two of the subsequent fronds.

The thickness of the stem increases suddenly and considerably above the fifth or sixth frond. This rapid growth in thickness takes place whilst the next younger fronds, the seventh to the tenth, continue in the state of buds. Owing to the vigorous and rapid peripheral development, the apical region of the stem becomes almost a flat surface, in the middle of which the outermost point of the stem protrudes (Pl. XXVI, fig. 15). Around it the youngest fronds are arranged spirally. Henceforth the end of the stem retains this form (Pl. XXVI, fig. 19; Pl. XXVII, figs. 3, 4).

The flattening of the terminal bud depends upon the fact that the superficial cells of the conical cellular mass divide repeatedly by septa parallel to the chord of the arcuate free outer wall—(a mode of cell-multiplication which increases continually from the apex of the cone to its

base where it suddenly ceases, and which is accompanied by a series of divisions proportionate in number to the increase of the circumference of the cone and produced by longitudinal septa radial to the axis of the stem)—whilst the division by transverse septa at right angles to those chordal longitudinal septa occurs proportionably seldom. The conical terminal bud grows upwards by the formation beneath its entire outer surface of a layer of cells having the form of a conical covering thicker towards the base, whilst the angle of inclination of the cone becomes continually narrower. At a latter period, after the formation of the rudiments of several cycles of fronds, the longitudinal growth of the stem is so much accelerated by the active extension of the cells of the axile tissue (accompanied by the formation of transverse septa in the peripheral cells) that it exceeds the previous increase in thickness. The cortical region is pushed outwards by the longitudinal extension of the middle of the stem, and passes from the form of a very blunt cone into that of a cylinder; this complete inversion of the mode of growth is caused by the change of direction of the expansion and multiplication of the cells. The process (which is common to all stems with flat terminal buds, *e. g.*, Polytrichum, Dracæna) is more easily seen in the slender stem-ends of the germ-plants and gemmæ of *Aspidium filix-mas* or *Asplenium filix-femina*, than in the stems of older individuals of the former plant which become too thick.

After the stem of the germ-plant has increased in thickness the arrangement of the subsequent new fronds changes from the $\frac{1}{3}$ to the $\frac{2}{5}$ arrangement. At the same time the distribution of the vascular bundles in the stem becomes different. At the place where the vascular bundle which passes into the last frond of the $\frac{1}{3}$ arrangement turns sideways, strings of the cambium which afterwards forms the vascular bundles separate themselves in the direction of each of the three next fronds, and run parallel to the longitudinal axis of the stem (Pl. XXVI, fig. 15). A transverse section of the stem at this spot exhibits three vascular bundles arranged in a circle (Pl. XXVI, fig. 16).

The rudiments of the vascular bundles which pass to all

the succeeding fronds are already formed whilst the fronds are still in the condition of very young buds, inasmuch as from the place where those vascular bundles which pass to the two next adjoining older fronds bend aside to make their way out of the stem, the cells of the bud-tissue are transformed into cambium-strings as far as the younger frond. Close under the place of insertion of the young frond the two rudimentary vascular bundles unite to form a single one (Pl. XXVI, fig. 9) which after passing through the stipes for a short distance splits again into two (Pl. XXVI, figs. 10, 11). A vascular bundle passes to the first frond from the fifth and sixth, and to the ninth from the sixth and seventh, and so on. Thus the vascular bundles of the young stem represent in their entirety a tubular net, with rather wide meshes,* from whose angles simple vascular bundles pass off to the fronds. A transverse section of the stem of a seedling of about a year old exhibits five vascular bundles enclosing a pith.

In the second year the plant develops itself much more vigorously. Its fronds attain a foot in length; their arrangement proceeds normally according to the $\frac{5}{13}$ arrangement. Henceforth several vascular bundles occur in each stipes. In old vigorous individuals as many as five pass from the knot of vascular bundles which corresponds with the place of insertion of each frond. The lowest and most vigorous of these bundles—which, as it originates out of the lower angle of the knot of vascular bundles, corresponds with the single bundle of the fronds of the one-year-old plant—passes near the hinder surface of the stipes, and divides into two close above the place of attachment of the frond to the stem, at the place where the protuberant enlargement of the stipes, characteristic of *Aspidium filix-mas*, begins (Pl. XXVII, fig. 6). Mature plants produce roots exclusively from these two vigorous bundles of the stipes. The stem, which in the first year of the germ-plant sends out all the roots, afterwards ceases to produce any. From the side angles of each knot of vascular bundles of the stem two thin vascular bundles pass off into the frond, and

* Mohl, 'Vermischte Schriften,' p. 115.

two rather more vigorous ones at a little distance higher up (Pl. XXVI, fig. 20). Both pairs run along the protuberant longitudinal ridges of the frond, the former pair behind, the latter in front (Pl. XXVII, fig. 7). The vascular bundles not unfrequently anastomose in the interior of the stipes. Hence it arises that transverse sections of the latter sometimes exhibit more than five vascular bundles.

The distribution of the vascular bundles within the stem remains essentially the same during the progress of the arrangement of the fronds, except that (as is manifest) the number of loops increases. The first frond of a cycle receives its vascular bundles no longer from the sixth and seventh, but from the ninth and eleventh of the preceding cycle; the sixth frond from the first and the third, the eighth from the third and fifth of the same cycle, and so on. Or to state it more shortly—the vascular bundles which pass from the right to the new fronds follow (when the turn of the spiral is normal, or to the right hand) the 3-numeral fronds; those which pass from the left follow the 5-numeral ones. Eight transverse sections of vascular bundles lie in one plane passing through the stem at right angles to the axis. In mature plants of *Aspidium filix-mas*, there is a periodicity in the development of the frond which is not found in the one-year-old seedling. The growth of the frond in the former is arrested in winter, but not so in the latter. The number of fronds which unfold in spring, and which all grow simultaneously from the end of May till October, is usually thirteen, corresponding with the number of the joints of a segment of the spiral in which the fronds are arranged. A similar state of circumstances is met with also in some other ferns, as in *Asplenium filix-femina*, where the number of fronds is usually eight or thirteen, and in *Aspidium spinulosum* and *Asplenium Trichomanes* where eight fronds are usually developed contemporaneously. As in *Pteris aquilina*, the rudiments of the fronds are formed two years before their unfolding. In the first year the stipes only is formed, and in the outermost fronds of the cycle about three or five of the pinnæ. In the second year the pinnæ of those fronds which are to

open in the spring are completed in all their parts, and after the second winter's rest they are fully developed. The younger fronds of the same season follow step by step in the same development until the month of June.

The commmencement of the formation of the vascular bundles takes place in the bud even of very vigorous specimens from the fifth-youngest frond in a backward direction, and thus, far above the point at which the longitudinal growth of the stem begins to exceed its growth in thickness. Thus the whole system of vascular-bundle-meshes lies at first in an almost horizontal, very flatly paraboloidal surface, close under the top surface of the stem, and nearly parallel thereto. It is only immediately below the apex that the number of the cells of the tissue of the stem underneath and within the net of vascular bundles is increased; lower down there occurs an expansion of these internal cells, their longitudinal diameter becoming from four to five times longer, and their transverse diameter from two to three times wider. It is only by this increase (caused by cell-expansion) of the bulk of the pith that the net of vascular bundles is lifted up by degrees and projected upon a cylinder. It is easily seen by counting the cells during and after the transition of the net of vascular bundles from the form of a paraboloid to that of a cylinder, that the increase in thickness of the stem is not caused by any subsequent new formation of parenchymatal cells either within the pith or in the neighbourhood of, or between, the rudimentary vascular bundles. It is only in front of the youngest rudimentary vascular bundles that a slight multiplication of the cortical tissue takes place, by division of the peripheral cells (Pl. XXVII, fig. 3).

If any radial section be taken through the longitudinal axis of the stem the side view thus obtained of the apical cell of the terminal bud is without exception three-sided (Pl. XXVII, figs. 3, 4). When viewed from above the upper surface of the same cell exhibits the like shape (Pl. XXVII, figs. 1, 2). Its form is therefore that of an inverted three-sided pyramid with an arched upper surface. The appearance shews (Pl. XXVII, figs. 1, 2,) that this cell divides repeatedly by septa, having three directions, and turned suc-

cessively to one of the lateral surfaces. As far as can be judged from numerous observations, the succession of these septa one after another is to the right hand, more seldom to the left, but always coincident with the spiral in which the fronds are arranged.

There is yet a second point in which the relation of the apical cell to its daughter-cells is affected by the frond-spiral. The apical aspect of the top cell of old specimens of *Aspidium filix-mas* is very rarely that of an equilateral triangle. One of the sides is usually considerably shorter than the two others, which latter are nearly of equal length. The outline of the apical surface is normally that of an isosceles triangle. Deviations from this form may be easily traced to the disturbances caused in the older lateral surfaces of the apical cell by the growth of the adjoining secondary cells. The one side of the triangle is formed by the upper edge of the youngest side-wall of the terminal cell, and the other side by that of the oldest side-wall of the same cell. The base is formed by the side-wall intermediate in age between the oldest and the youngest.

The relation of the length of this base to the younger of the two sides is in most cases a definite one. The following series of measurements will show this. The younger of the two longer side-walls of the apical cell is the one always measured. Some of the measurements were made on the apical cells of buds which had been separated by a transverse section from the older portion of the stem, and simply cleansed from the adherent mucilage and scales. The greater part of the measurements, however, were made on the transparent membrane formed by the free outer walls of the superficial cells of the bud. These walls have a much stronger consistence than those of the inner tissue of the bud. After a little practice with the microscope it is not difficult to scrape out from the inside of the terminal bud the mass of internal parenchyma, consisting of delicate cell-walls and cell-contents, so as to leave the outer walls in the form of a connected, slightly arched membrane—(the epidermis, improperly so called, of the young portions of the plant). The lines of contact of the cell-walls which have been attached to this membrane are most dis-

tinctly marked upon the latter in the form of slightly protuberant ridges, and admit of the most accurate measurements. Each of the following is the mean of at least five measurements which did not differ from one another by more than half a micro-millimeter.*

Measurements of the apical cells of Ferns having the $\frac{5}{13}$ frond-arrangement.

—	Base.	Side.	Relation of the two.
	M.M.M.	M.M.M.	
Aspidium filix-mas, Spiral right .	33.6476	47.1618	1 : 1.401
" " " " .	39.912	56.542	1 : 1.416
" " " " .	43.3104	61.0986	1 : 1.401
" " " " .	45.2312	63.7098	1 : 1.408
" " " " .	46.564	66.52	1 : 1.41
" " " " .	49.89	70.6773	1 : 1.416
" " " " .	51.8504	73.6386	1 : 1.42
" " " " .	52.859	75.0198	1 : 1.419
" " " " .	55.7116	78.593	1 : 1.41
" " " " .	55.7116	79.5336	1 : 1.427
" " " " .	55.9874	78.593	1 : 1.403
" " " " .	56.542	79.824	1 : 1.411
" *spinulosum* " left .	36.6076	51.3022	1 : 1.401
" " " " .	40.1194	56.4582	1 : 1.406
" " " right .	43.0526	60.3246	1 : 1.401
" " " " .	43.0526	60.8408	1 : 1.413
" " " " .	44.0838	61.7421	1 : 1.4
" " " left .	52.0756	73.2152	1 : 1.407
" " " right .	52.6778	74.5487	1 : 1.401
" " " " .	52.9536	75.5692	1 : 1.428
Aspl. filix-fem. " " .	33.26	46.564	1 : 1.4
		Mean . . .	1 : 1.4094

This proportion of the base to the sides is that of an equilateral triangle with an apical angle of 69° 13′ 53·3″, and whose angles at the base are 41° 32′ 13·4″; angles which very nearly approximate to those of a triangle which is bounded by the chords of two arcs of 138° 27′ 41·53′—(two successive steps of the smaller divergence of the $\frac{5}{13}$ frond-arrangement)—and by the line uniting the free terminal points of these chords, which line is the chord of an arc of 83° 4′ 36·94″, being the difference between the larger and the smaller divergence of the $\frac{5}{13}$ arrangement. The apical angle of such a triangle is 41° 32′ 18·47″; each of

* 1 m.m.m. = 9·0001 millim.

the angles at the base is 69° 13′ 50·765″; the relation of the base to one of the sides is 1 : 1·4067. The divergence of these numbers from the measurement falls within the limits of probable error.* The conformity of the angle of the apical cell of the stem with the divergence of the appendicular organs is not limited to the $\frac{5}{13}$ arrangement. The calculated relation of the shorter side of the triangular apical surface of the terminal cell to one of the longer sides is:

In the	$\frac{2}{5}$	arrangement	1 : 1.618
„	$\frac{3}{8}$	„	1 : 1.307
„	$\frac{5}{13}$	„	1 : 1.4067
„	$\frac{8}{21}$	„	1 : 1.3683
„	$\frac{13}{34}$	„	1 : 1.3799
„	$\frac{21}{55}$	„	1 : 1.3294

The observed relations are—

—	Base.	Side.	Relation of the two.
	M.M.M.	M.M.M.	
Asp. filix-mas $\frac{3}{8}$ arrangement, Spiral right .	56.9738	74.2464	1 : 1.307
„ „ „ „ (seedling)	27.8558	36.6814	1 : 1.316
„ „ „ „ „ .	36.1298	47.7134	1 : 1.3216
„ $\frac{8}{21}$ „ „ right .	63.161	86.1052	1 : 1.363
„ $\frac{13}{34}$ „ „ „ .	63.4386	90.23	1 : 1.381

It would be natural to attempt to explain this phenomenon by the supposition, that the angle which a new septum of the apical cell forms with the next older side wall, bears a relation to the angle of divergence of the frond arrangement, inasmuch as it equals the half of the latter angle. The necessary result of this would be, that

* I considered it much better to calculate the angle of the apical surface from the length of its sides than to measure it directly with the goniometer, as the former process gives a more certain result. The credibility of each method depends upon the same circumstances as those upon which, in the determination of phyllotaxis, the relative credibility of the results obtained by the direct measurement of the angle of divergence and by the calculation of the latter from the number of the turns, depends. The number of measurements might easily have been increased, but it seemed advisable to exclude all the cases in which the imperfect parallelism to the apical surface of the stem of the section separating the outermost apex of the flat bud from the remaining tissue, might have given rise to mistakes.

in each mode of frond arrangement following upon the $\frac{2}{5}$ arrangement, such as $\frac{5}{13}$, $\frac{8}{21}$ and so forth, the form of the apical surface of the cell of the first degree would be that of an isosceles triangle. Each cell of the second degree might be treated as the primary mother-cell of a frond, to be produced by the further development of the cells derived from the secondary cell. This supposition would however require that the four sided apical surface of each cell of the second degree, should, immediately after its production, be considerably wider on the hinder edge than on the fore edge. The excess of the length of the hinder edge over that of the fore edge would be determined by the difference between the apical angle and one of the side angles of the upper surface of the cell of the first degree. It would necessarily bear the same proportion to the second youngest side of the apical surface of the compound figure formed by the cell of the first degree and the youngest cell of the second degree, as the sine of the apical angle bears to that of one of the side angles. Consequently each cell of the second degree must, immediately after its production, be wider at the hinder end than at the fore end to the following extent in each respective case, that is to say,—in the $\frac{1}{2}$ arrangement to the extent of about the whole length of its front wall and of the oldest wall of the apical cell which represents its prolongation,—in the $\frac{3}{8}$ arrangement to the extent of something more than the half (0·5412) of this length,—in the $\frac{5}{13}$ arrangement to the extent of about $\frac{7}{10}$ (0·70081) of the same.

Observation entirely upsets the above supposition. It is true that in older cells of the second degree, especially in those which are already several times divided, the outer side wall normally diverges from the inner one. But the younger the cells of the second degree which are subjected to examination, the more nearly do their side walls approach to parallelism, until at last it is manifest that the earliest septa of the cell of the first degree appear exactly parallel to the oldest side wall of the same cell (Pl. XXVII, fig. 1). It is plain from this that in point of fact the supplementary expansion and the multiplication of the cells of the second degree proceed step by step from back to front

(by which gradual advance the broken, sharply-angular succession of these cells is converted into a spiral) but that there is no perceptible divergence of the newly formed septa of the cell of the first degree from the oldest opposite side wall of this mother-cell.

There is a second series of facts which militates not less decidedly against the above assumption, viz., the occurrence, although a rare one, of apical surfaces of cells of the first degree which exhibit angles not corresponding with those of the frond-arrangement. The following instances have been observed, and they are the only ones obtained in a long series of investigations:—

—	Length of the oldest side wall of the apical cell.	Length of the youngest side wall of the apical cell.	Relation of the two.
Asp. spinulosum, $\frac{5}{13}$ arrangement, Spiral right	60.583	83.0116	1 : 1.37
" " " " " "	56.3293	76.3088	1 : 1.355
" " " " " left	52.7201	68.783	1 : 1.307
" " " " " right	45.5017	52.4623	1 : 1.152
" " " " " left	59.5518	61.0986	1 : 1.026
" *filix-mas*, " " " right	55.427	73.9886	1 : 1.335
" " $\frac{8}{21}$ " " "	71.1528	88.1676	1 : 1.239
" *spinulosum*, $\frac{3}{8}$ " " "	69.8638	75.7932	1 : 1.088
" *filix-mas*, $\frac{5}{13}$ " " "	88.4254	85.074	1 : 0.961
" " " " " "	69.0904	63.161	1 : 0.913

In the greater number of these irregularly shaped cells their size is very remarkable. In none of the foregoing tables did the base of the triangle attain the length of 64 m. m. m., a length which is here often surpassed.

But the measurements of those apical cells in which the length of the oldest side-wall considerably exceeds that of the youngest, are very instructive. Taken in connexion with the fact, that in by far the greater number of instances the angles of the apical cell correspond with the divergence of the frond-arrangement, these phenomena indicate that after each division the apical cell does not become enlarged equally in all directions so as to attain the size which it had before the division, but that the expansion which

ensues takes place, if not exclusively, at all events principally, in a direction at right angles to the septum last produced. This septum which, at the instant of one division, forms one of the sides of the isosceles triangle represented by the upper surface of the cell of the first degree, is, until the next division, far surpassed in longitudinal growth by the two other side walls of the apical cell, so that the latter then constitute the sides and the newly-formed septum the base of the triangle. The new division is produced by a septum which is parallel to the second side wall of the apical cell, which side-wall at the time of the preceding division was the longer one, and which in the mean time has become elongated and displaced.

The diagram given in Pl. XXXII, fig. 5, of the mode of succession of four such divisions of the apical cell of a bud with the $\frac{5}{13}$ arrangement, will explain the above suggestion.

The triangle enclosed by the lines 1, 2, 3, represents the apical cell before the first of these divisions; the line 4 represents the course of the dividing membrane. This cell (which we will designate with the figure II until the next division) now expands to the left: the line 4 now becomes the base of the triangle; the line 1, increased by the line 1^{II} becomes one side of the triangle, and the line 3, displaced to 3^{II} and lengthened, becomes the other side of the triangle. The next division is represented by the line 5. This line becomes the base of the upper surface of the cell, which is enclosed by the lines 3^{II}, 4, and 5, and which expands again to the left. By this expansion the line 3 becomes the line 3^{III}, and the line 4 becomes 4^{III}. The line 6 represents the third division. The apical cell is now first bounded by the lines 4, 5, 6. By a fresh expansion of the cell the line 5 is increased by the line 5^{IV}, 4 is shifted to 4^{IV}, 2 to 2^{IV}, and 1 is extended to 1^{IV}.

Pl. XXXII, fig. 6, exhibits the somewhat complicated mode of arrangement and displacement of the cells of the second degree after three more such divisions of the apical cell.

All the above facts can easily be brought under the one point of view of the above supposition. The latter explains

the frequency of the correspondence in form of the upper surface of the cell of the first degree with the frond arrangement, as well as the rarity of the deviations from this form. Moreover, the observation confirms the consequent backward curvature of the lines uniting the projecting angles (which are turned to the same side) of the different courses of the successive cells of the second degree around the axis of the stem;—which lines represent three similar turns of the frond-spiral. The above opinion is further supported by the fact, that the expansion and displacement supposed to occur in the apical cell, must necessarily follow from the enlargement and multiplication, progressing gradually from the older to the younger ones, of the cells of the second degree. The marginal angles of the lateral surfaces of the cell of the first degree, must, in the direction of the ascending spiral which represents the course of the divisions, become more acute at the fore edges, and more obtuse at the hinder ones, if—as observation proves—the multiplication of the older cells of the second degree in the direction of a tangent to the stem is more active than that of the youngest cells. In this process the apical cell may be looked upon as to a certain extent passive.

The supposition of a high degree of expansive and formative power in the walls of the young cells of a portion of a plant in process of development, is indispensable for the purpose of explaining the change in the position and form of the individual cells, which is caused by the growth of the entire portion of the plant, and by the influence of the expansion (and the multiplication of the older cells and masses of cellular tissue) upon the younger ones, and conversely. In the terminal bud of ferns expansion and multiplication of the secondary cells, and of the groups of cells produced by their divisions, advance in an ascending spiral from below upwards. In the neighbourhood of the apical cell this expansion occurs at an early period (and is consequently more advanced and productive of greater results) in the oldest wall which forms the base of the upper surface of the cell, and in the next oldest, whose margin forms the penultimate side of that surface. The growth of the apical cell, which, between

each two divisions always increases to nearly the original size, become especially active in the direction of the marginal angle formed by these two side-walls. This will cause its form to vary more and more in the manner above pointed out, until the relation between the angles required by the hypothesis is attained. It is easy to imagine that any excess of aperture is prevented by the proportion of the rapidity of the progress of the multiplication of the older secondary cells to that of the youngest.

In the course of the long inquiries leading to these results, I met with only one isolated fact which militated against the conclusions arrived at. I found the apical cell of a terminal bud of *Aspidium spinulosum*, the base of whose upper surface measured 41·248 m.m.m., and each side 97·808 m.m.m. The stem, which had the left-handed $\frac{5}{13}$ arrangement of the fronds, was growing at the edge of a ditch, amongst a mass of briars, being half buried in the earth, and directed downwards: the joints of the stem were unusually elongated. It is probable that the plant was in an abnormal, perhaps in a diseased condition.

The two-edged form of the apical cell, and the bilinear arrangement of the fronds, of *Pteris aquilina*, have been already observed upon. The same coincidence is always met with (as far as present observations extend) in *Niphobolus rupestris* and *N. Lingua*, in *Polypodium punctulatum*, *P. cymatodes*, and *P. aureum*, and very frequently in *P. vulgare* and *Dryopteris*.

The determination of the cell-succession in the apical region of the leaf-buds of phænogamous plants is attended with considerable difficulties. The minuteness of the elementary organs is the least obstacle; a more formidable one, especially in the Coniferæ and Dicotyledons, is the very early occurrence of rapid and vigorous multiplication of the secondary cells of the flat end of the bud. It is not always that the terminal cell of the bud can be ascertained with certainty. Where however this was done the form of this cell corresponded with the phyllotaxis; it was two-edged in the grasses (*Secale cereale*, *Phragmites arundinacea*) and in species of Iris; and often of the same shape in trees with decussate leaves (*Acer*, *Fraxinus*, *Cupressus*). Here

however cases occurred, though less frequently, of triangular upper surfaces with a very acute apical angle. These irregularities possibly depend upon the fact of the occurrence in each internode of a gradual transposition, a deviation of about 90°, of those septa of the apical cell of the bud, which are turned towards the surfaces of the leaves.

Trees with imperfect 3-numeral phyllotaxis always exhibited three-sided apical cells with one shorter edge. In *Robinia Pseudacacia* (phyllotaxis $\frac{2}{5}$) the following measurements occurred :—

The base of the triangle.	One of the sides.	
9.9288 m.m.m.	15.4448	= 1 : 1.555
10.121 „	16.2936	= 1 : 1.689
9.875 „	15.9975	= 1 : 1.62
	Mean . .	= 1 : 1.634

This result corresponds as nearly with the relation required by calculation, viz. 1 : 1·618, as could be expected, considering the errors in measurement likely to arise from the minuteness of the objects. Even if the first of the above measurements may not be attributed to the displacement of the apical cell between two divisions, it would only be necessary to introduce a correction of about $\frac{1}{6000}$ millimeter in the first, and the same in the second (where the proportion is too large), in order to make the observed measurements correspond with the calculated ones.

The following are farther measurements of apical cells :—

—	Base.	Side.	Relation of the two.
	M.M.M.	M.M.M.	
Pinus Abies, phyllotaxis $\frac{8}{21}$ turned to the right	13.79	18.7544	= 1 : 1.36
„ „ „	15.8569	21.5124	= 1 : 1.3566
„ „ „ $\frac{13}{34}$ turned to the right	14.6174	20.4192	= 1 : 1.397
Pinus Balsamea, phyllotaxis $\frac{8}{21}$ turned to the right	13.8451	19.0302	= 1 : 1.375
„ „ „	14.3416	19.488	= 1 : 1.359
„ „ „	13.5422	18.4615	= 1 : 1.363
Zamia longifolia, phyllotaxis $\frac{5}{13}$ turned to the right	27.58	38.612	= 1 : 1.4

The first division—at right angles to the free outer surface—of the cells of the second degree of *Aspidium filix-mas* and *A. spinulosum* is produced sometimes by a septum parallel to the front surface, *i. e.*, the surface by which the cell of the second degree is connected with the cell of the first degree (Pl. XXVII, fig. 2, Pl. XXXII, fig. 4), and sometimes by a longitudinal septum meeting the front wall at an angle of about 70° (Pl. XXVII, fig. 1). In the former case the second mode of division follows upon the first, in the latter case the first mode of division follows upon the second; the final result is the same in both cases. The further divisions of the cells of the terminal bud are subject to not less stringent rules. The tendency to transform the zigzag line of succession of the generations of cells resulting from each cell of the second degree into an uniformly ascending spiral line, manifests itself especially in the frequent occurrence of three-jointed groups of cells which originate in the following manner—the septum produced in a cell of the outer surface is parallel to no one of the side walls, but cuts two of the side walls of the mother cell which form an edge, in such manner that the latter is divided into a smaller daughter-cell with a three-sided outer wall, and a larger cell with a four-sided outer wall. The latter cell is divided again by a septum almost at right angles to the one last formed. Instead of one cell of the n^{th} degree there are now three: one of the $\overline{n+1}^{th}$ and two of $\overline{n+2}^{th}$ degree.

The cell-succession of the terminal bud, and the form of the terminal cell which is possibly the result not the cause of such cell-succession, are manifestations of the same power of growth, by which the arrangement of the fronds on the axis is determined. After long extended and often repeated observations of the attendant circumstances, the conclusion will not be premature, that the power by which the form of the growing portions of plants is determined, is manifested in the details of the cell-multiplication by so much the less in proportion as the organs in question are composed of a greater number of cells. The main directions in which the cell-multiplication takes place are fixed: the number however and mode of succession of the cell-

divisions in these directions varies within rather wide limits.*

The younger portions of the bud of *Aspidium filix-mas* are enveloped in transparent mucilage as is usually the case with all buds.† Owing to the very imperfect exclusion of the outer air from the terminal bud of this fern, in which the punctum vegetationis is only covered by the connivent scales of the older parts, this mucilage is often partly dried up, and forms a structureless membrane, granular on the outside, covering the top of the bud; precisely similar to that which is seen on the youngest parts of the fronds of Anthoceros.‡ In order to obtain a clear view of the top of the bud it is necessary to remove this membrane, which is a laborious and uncertain operation.

The small scales (whose development differs in no essential particulars from that of the similar organs in *Niphobolus rupestris* to which we shall afterwards refer), make their appearance on the terminal bud very far above the point at which the cellular increase of the stem in thickness terminates, but never above the place of origin of the youngest frond (Pl. XXVI, fig. 14; Pl. XXXII, fig. 4). This holds good in Aspidium as well as in Pteris, Polypodium, &c. According to Nägeli's definition of leaves and hairs,§ the scales would undoubtedly belong to the former, as I also formerly assumed to be the case.‖ On the other hand a conclusive method of distinguishing

* This conclusion is the same as that which I arrived at on a former occasion from observations on Isoetes (see vol. ii of the 'Abhandl. der K. Sächs. Ges. d. Wiss.' p. 161). The statement there made, that all the septa—turned in one of the three directions—of the apical cells of the three-furrowed Isoeteæ are at right angles to a plane passing through that indentation of the stem which is nearest to them, is too positive and general. Nevertheless the observations, the number of which was limited by the paucity of the materials, certainly show, that all the septa seen were turned towards one of the indentations; no one of them was turned towards the space intermediate between two indentations. This fact may have some connexion with the high ratios of the numbers representing the phyllotaxis of those species of Isoetes.

† See 'Vergl. Unters.,' p. 82, note.

‡ See 'Vergl. Unters.,' Pl. i, figs. 8, 9.

§ 'Zeitschr. f. Wiss. Botanik,' Heft 3, 4, p. 185. The leaf is formed on the outside at the top of the stem, close under the apical cell, before the growth in thickness by peripheral cell-formation is ended . . . . . The hair, &c., is formed on the outside on an epidermal cell by growth of the latter after the termination of the peripheral cell-formation.

‖ 'Vergl. Unters.,' p. 87.

between the two is arrived at, if the difference between hairs and leaves is sought for in the facts that the youngest hairs are never seen below the first visible rudiments of the leaves, and that leaf-formation on the axis always precedes the formation of hairs. By trusting to these characters the observer will never be in doubt, in any case where the axis of the plant exhibits both these forms of appendicular organs. The scales of ferns therefore, as well as the hairs in the buds of mosses and liverworts, fall under the definition of hairs, and the fronds consequently under that of leaves.*

The formation of a frond commences thus—one of the superficial cells of the terminal bud, distant from the next older frond by the angle of divergence of the frond-arrangement increases in size, and becomes arched outwards in a papillate manner (Pl. XXVII, fig. 4; Pl. XXXII, fig. 4). In this cell there commences a series of divisions which are repeated continually in the apical cell by means of septa turned to the right and left towards the future margins of the frond. The secondary cells multiply in all three directions more vigorously on the hind surface of the frond, so that the latter is converted into a somewhat slender cone bent over towards the fore part. Septa are now produced in the apical cell, turned towards the fore and hind surfaces of the frond, and alternating with others turned towards the lateral margins. The further formation of the frond, the development of its blade, takes place in the manner pointed out in *Pteris aquilina*.

In the mature plant of *Aspidium filix-mas* roots (as we have already said) are no longer formed on the stem itself, but exclusively on the protuberant swollen portion of the

* Two of the main grounds formerly adduced to prove that the scales were of the nature of leaves, and the fronds of the nature of branches, have been set aside. Kunze's statement, that the delicate bodies, resembling the fronds of Trichomanes, found at the base of the stipes of *Hemitelia capensis* are transformed scales, is erroneous, as has been already observed. They have nothing in common with scales as may be seen at once by the examination even of a dead stem. The course of the vascular bundle within them is conclusive to show that they have been formed in the earliest stage of the frond, even before the commencement of the formation of the blade of the latter. I have latterly arrived at a very clear view of the growth in the Ophioglosseæ. I formerly thought that it must be considered to consist of a successive series of adventitious buds. I now find that the Ophioglosseæ agree essentially with the Polypodiaceæ.

stipes. They originate here from the vascular bundles which run on the hind side of the stipes, parallel to the longitudinal ridges of the latter. Usually two roots are formed on each stipes. Every longitudinal and transverse section of the root-cell of the first degree appears triangular. Its form is that of a low three-sided pyramid. It divides by means of a concave septum turned towards its slightly convex basal surface, and by this means lenticular cells are formed, each of which becomes the mother-cell of two of the cap-shaped cellular layers of the root-cap. The lenticular cell divides by longitudinal septa into four cells standing cross-wise (Pl. XXVII, fig. 10), after which transverse septa are formed. In the middle of the circular cellular layer, the further division by longitudinal septa occurs more rapidly and more frequently than at the edges, by which means the cellular surface assumes its cap-like shape. Between the older of these cellular layers, whose outer walls become very much thickened, intercellular spaces filled with air make their appearance; this is the first commencement of the falling off of the cellular layers of the root-cap, which decay by degrees from the outside. Each division which is produced by means of a concave septum turned towards the basal surface of the cell of the first degree, is followed by three divisions of the latter, by means of septa successively parallel to each of its three lateral surfaces. The three cells of the second degree thus formed, and which stand in a triangle, divide by means of longitudinal and transverse septa, the division being more active in that portion of them which is more distant from the longitudinal axis of the root. The short-celled tissue here formed becomes the cortical layer, whose early growth is afterwards overtaken by the rapid longitudinal expansion of the axile cellular tissue of the root during the transformation of the latter into the central vascular bundle.*

It is only in very rare instances that the terminal bud of the stem of *Aspidium filix-mas* divides by true forking of the

* In consequence of my having examined sections which were not truly axile, I was led to assume that the lenticular cells of the interior of the root of *Equisetum variegatum* ('Vergl. Unters.,' pl. xviii, fig. 3), as well as the primary cells of one of the layers of the root-cap, were root-cells of the first degree.

punctum vegetationis. The multiplication of shoots by means of adventitious buds is proportionably more frequent. These buds always originate on the back of the stipes, at the place where the protuberant swelling of the latter passes off into the more slender upper portion. After the removal from the stipes of the thick covering of scales, the earliest conditions of the adventitious buds may be seen in the form of a disk surrounded by an annular furrow and having a slight protuberance at its middle point which represents the apex of the new axis in process of formation. Somewhat later, other protuberances, being the rudiments of fronds, are seen, arranged in a circle round the central one (Pl. XXVII, fig. 5). Whilst on the mother-plant the new shoot begins to send forth roots independently (Pl. XXVII, fig. 6). The vascular bundles which pass to it from the vascular bundles of the frond on which it is produced, unite at its place of attachment so as to form a closed ring from which their distribution in knots answering to the insertions of the fronds commences (Pl. XXVII, fig. 7). Such adventitious buds are formed on vigorous plants in fertile habitats at about every twelfth frond, and much more frequently in plants growing in dry situations.*

Aspidium spinulosum comports itself in all its parts like *Aspidium filix-mas*. The adventitious buds are here met with very near the base of the stipes. The scales bear at their apices, and frequently also on the teeth of the margin, very swollen, oval, or pear-shaped cells with mucilaginous contents; a phenomenon which is also seen in *Aspidium Oreopteris, Asplenium filix-femina, Struthiopteris germanica* and other ferns.

Asplenium filix-femina; Asplenium Bellangeri; Struthiopteris germanica; Nephrolepis undulata; Nephrolepis splendens.—The above-named ferns agree entirely in the principal features of vegetation, viz., in the form and mode of multiplication of the cells of the terminal bud; in the position of the frond-cells of the first degree with regard to the apical cell of the terminal bud; and in the arrangement of the

* It is probable that Schleiden had these buds in view when he spoke of this fern as having axillary buds ('Grundzüge' 2 Aufl., vol. ii, p. 87), which in *Aspidium filix-mas*, as in all European ferns, are absolutely unknown.

vascular bundles in the stem. *Asplenium filix-femina* is distinguishable by the more slender form of the terminal bud, the growth of which in thickness terminates at the fourth set of cells, (reckoning downwards and sideways from the apical cell), the produce of one of the cells of the second degree, so that the frond-less apex of the stem is elevated considerably above the earliest rudiments of the fronds (Pl. XXXIII, fig. 2). A further peculiarity of this plant is that only one vascular bundle enters each stipes from the upper angle of each knot of vascular bundles. For a considerable distance this bundle is simple; it then divides into two, and further up into several strings. The status which in *Aspidium filix-mas* only occurs whilst the plant is young, that is to say only in the one year old plant, is maintained here during its whole life. Underneath the place where the vascular bundle of the stipes exhibits its first ramification, one root is normally produced; each frond has only one, which is developed in a plane passing through the median line of the frond. This circumstance greatly facilitates the investigation of the earliest stages. In well-made longitudinal sections, close outside the rudimentary vascular bundle of the frond, there may be seen the primary cell of the appurtenant root, by the multiplication of which in the manner pointed out in *Aspidium filix-mas*, the root-cap and the permanent cylindrical portion of the root are produced (Pl. XXXIII, figs. 4, 5). The tissue of both halves of the growing root, as well as the cells of the root-cap, are, whilst in this early state, in intimate parenchymatal connexion with the cortical cells of the stipes. Afterwards, shortly before breaking forth from the hind surface of the stipes, the boundary between the root-cap and the cells before it becomes sharply defined (Pl. XXXIII, fig. 6) without however any rupture of the tissue, or the appearance of any inter-cellular space. The few cellular layers of the stipes anterior to the apex of the young root, are gradually displaced and dissolved, not broken through; the cuff-like margin, which is formed from the cellular tissue of the mother-portion of the plant, and which is so remarkable on the adventitious roots of many Monocotyledons, is wanting here.

Adventitious buds are very rare in *Asplenium filix-femina*; it would seem that they never occur when the plant is growing naturally. However at the base of the stipes of a frond which had been torn off and kept for some time in a closed bottle in moist air, I saw adventitious buds produced underneath the place of attachment of the roots (Pl. XXXIII, fig. 1). On the other hand the forking of the apex of the stem by division of the frond-less terminal bud is in this fern quite a normal process; it is the usual asexual mode of multiplication of the plant which it would seem occurs at tolerably regular intervals. The observer will seldom fail to find the bifurcation of the stem in old plants; specimens often occur with from four to nine heads.

In *Struthiopteris germanica* * the formation of numerous adventitious shoots is added to the other peculiarities already mentioned.† As in *Aspidium spinulosum*, they originate on the outside, at the base of the stipes, close above its insertion into the stem. The first commencement of their formation occurs unusually early, long before that of the blade of the frond. In their first development they are directed obliquely downwards (Pl. XXXIII, figs. 7, 8).

The copious production of adventitious buds on all parts, even on the ramification of the blade of the frond, is very remarkable in *Asplenium Bellangeri*. The mode of development is essentially the same as in *Aspidium filix-mas*. Here also the new shoots do not originate in the interior of the tissue of that portion of the plant which produces them, but outside, on its outer surface.

It is well known that the species of Nephrolepis send forth long thin runners, whose ends, in *Nephrolepis undulata* and *N. tuberosa*, swell into knobs.‡ The stolons originate from adventitious buds, which are produced apparently on the stem, at that part of the base of the frond which amalgamates with, and forms a bark to the stem (Pl. XXXIV, fig. 3). The runners are one third of a line thick, and sparingly clothed with pale yellow scales;

* On the distribution of the vascular bundles, see Schacht, 'Pflanzenzelle,' Pl. xv, fig. 3—6.

† See Braun, 'Verjüngung,' p. 115.

‡ Kunze, 'Bot. Zeit.,' 1849, p. 881.

they root here and there, and are traversed by a vascular bundle. The apical cell of the terminal bud is always two-sided in *N. undulata*. On the thicker stolons of *N. splendens* it appears to be frequently three-sided. In *N. undulata* it first assumes this form when the apex of the runner begins to form a knob. Within the swelling mass of parenchyma the central vascular bundle, which has hitherto been simple, becomes branched (Pl. XXXIV, fig. 1). The bundles are henceforth arranged in a circle concentrical with the periphery of the knob.

As far as my observations extend, the vegetation of the terminal bud ceases with the complete formation of the knob, which is about an inch long.* The arrangement of the cells admits of the observation of their mode of cell-multiplication, if followed out in the same manner as in the end of the stem of *Aspidium filix-mas*. The contents of the cells, as well as those of the numerous rudiments of withering scales by which they are surrounded, become transparent. The knob sends forth fresh adventitious buds, which originate in numbers on its lateral surfaces (Pl. XXXIV, fig. 2). Soon after the development of these shoots the knob decays.

Polypodium, Niphobolus.—The species of Niphobolus, which I have examined (*N. rupestris* and *N. chinensis*), as well as several foreign species of Polypodium (*aureum, punctatum, cymatodes*), all exhibited the two-edged form of apical cell answering to the bi-linear frond-arrangement. In *Polypodium vulgare* it was otherwise. Here the terminal bud, when viewed from above, exhibits sometimes the form of the cell of the first degree and the arrangement of its next derivatives as in *Aspidium filix-mas* (Pl. XXXIV, fig. 6); sometimes (and most frequently) the two-edged form of the upper surface of the apical cell (Pl. XXXIV, fig. 5); sometimes forms which may be looked upon as intermediate between the two, inasmuch as the free outer wall of the cell of the first degree has the shape of a triangle, whose sides are more than three times the length of the base. Deviations from the typical bi-linear frond-arrangement are not un-

* This is opposed to Kunze's statement. He describes the further development of the apex of the bud, l. c., p. 882.

common in this species. They occur very frequently in plants which grow in places having a comparatively small amount of moisture, as is the case usually in an open plain. The frond-arrangement oscillates unsteadily between $\frac{1}{2}$ and $\frac{1}{3}$. Similar deviations occur in *Polypodium Dryopteris*.

The walls, by whose appearance in the first cell of the rudimentary frond the formation of the stipes commences, are radial, not tangential to the axis of the stem (Pl. XXXIV, fig. 4), agreeing in this respect with those of *Aspidium filix-mas*, and differing from those of *Pteris aquilina*. At the slender ends of the stems of *Niphobolus rupestris* and *N. splendens*, the development of the scales may be very conveniently traced. This development takes place at some little distance underneath the apical cell of the stem. The formation of the scales begins at a distance of eight cells from the top, reckoning downwards, by the formation of a papillate protuberance of the free outer wall of a cell of the circumference (Pl. XXXII, fig. 9). The protuberance is soon cut off from the original cell-cavity by a transverse septum. The appearance of a new transverse septum then divides the cell, which is already much flattened laterally, into an upper and a lower cell (Pl. XXXII, fig. 10). Repeated transverse divisions, not only of the apical cell, but also of the interstitial cells (Pl. XXXII, figs. 11, 12), transform the rudiment of the frond into a short series of low cells with an elliptical basal surface. The phenomena which become visible from these divisions, and especially the gradual dissolution of the primary nucleus of the dividing cell and the appearance of two new nuclei in its place, are precisely the same as those which are observed in the multiplication of the cells of the hairs of phænogamous plants (Pl. XXXII, fig 11).

The cells of the lower portion of the young frond now divide by longitudinal septa which coincide with the median line of the frond. These longitudinal septa are perpendicular to the surface of the frond, like the walls of almost all the cells which take part in the formation of the scales of ferns. The division progresses from the base of the frond towards its apex, extending in *Niphobolus ru-*

pestris to about the sixth, in *N. splendens* as far as the third cell from the apex, reckoning backwards. The uppermost cells of the frond, those into which the above division does not extend, now expand considerably lengthwise, the expansion commences with the apical cell and the others follow step by step (Pl. XXXII, figs. 13, 14). The termination of the multiplication of these cells is manifested by the thickening of their walls, and by their contents becoming transparent. On the other hand a partial, very considerable multiplication, ensues in the remaining cells of the frond. It is most considerable in the cells at the base, where the divisions by means of septa at right angles to the longitudinal axis of the frond are most frequently repeated, alternating with divisions parallel to such axis. The activity of the cell-multiplication diminishes continuously towards the apex of the frond. The divisions first cease in the cells of the upper half of the frond, which become elongated at the earliest period and to the greatest extent. The division of the cells of the frond by means of septa parallel to the longitudinal axis, appears not to be contemporaneous; it is repeated oftener, and extends nearer to the apex of the frond in one longitudinal moiety of the frond than in the other (Pl. XXXIII, fig. 8).

Owing to the gradual increase in breadth of the base of the frond, its cells in *Niphobolus rupestris*, *Nephrolepis splendens*, and *Polypodium aureum*, do not amalgamate with the cells of the circumference of the stem with which they are in contact. The place of attachment of the frond does not become wider, and moreover consists, even when the frond is perfected, of only two cells, which have been produced by the division by means of a longitudinal septum of the undermost cell of the rudiment of the frond. The cells of the free margin of the base of the frond multiply actively in many species (as for instance in *Niphobolus rupestris* and *N. splendens*), through division by means of septa parallel to a tangent to the circumference; those cells which adjoin the place of attachment of the frond and the angle of the lateral margins multiplying less actively than those between them. The base of the frond thus becomes

heart-shaped. The cells of the place of attachment, and often also those near it, divide, when the frond is almost perfect, by means of septa parallel to the surface of the frond (Pl. XXXIV, fig. 7). The cells of the lateral margins of the leaf often grow into delicate little teeth, which are usually curved backwards.

Scales which run through all the stages of development here represented are found not only on the principal axis of the plant but also on the lower portion of the frond. In the greater number of ferns the bases of the fronds exhibit scales at least in their youth. The arrangement of the scales both on the principal axes and on the fronds is governed by well-defined rules.* The reason why the arrangement is often undistinguishable on the fronds is that after the last important longitudinal expansion of the stipes individual scales fall off abnormally much earlier than the neighbouring ones.

In the earliest stages of *Polypodium vulgare* scales are found whose almost circular form indicates the tendency to assume the shape of a shield which is ultimately arrived at by the exuberant growth of the hinder margin, in which growth those daughter-cells take part which are derived from the primary cell, which after numerous divisions by means of longitudinal septa has become the attachment-cell (Pl. XXXIV, fig. 7).

The separation of the vascular bundles from the rest of the tissue of the stem, and the formation of roots from them, take place as in Aspidium and Pteris. In *Polypodium vulgare*, as in *Polypodium aureum*, the vascular bundles run off into a cylindrical annular net of meshes, which have no immediate relation to the insertions of the fronds.†

Platycerium Alcicorne.—The first frond of the germ-plant is erect and fleshy, having the shape of a spatula, and being slightly bent over behind. It is clothed with the stellate hairs characteristic of the plant, and has but few scales. The latter are more abundant on the young

* For instance, on the principal axis and fronds of *Niphobolus chinensis* the arrangement is $\frac{2}{5}$. The regularity of the arrangement is beautifully shown on the procumbent stem of *Polypodium aureum* by the little depressions, of which each one indicates the place where a scale has been attached.

† See V. Mohl, 'Vermischte Schriften,' p. 115.

stem, and are remarkable for their rapid development, especially in thickness, even in the early youth of the plant. The fronds which follow the first frond differ remarkably in form, direction, and structure. Their outline is circular or reniform; they are developed in a horizontal direction, bending backwards and downwards to such an extent from the point of attachment, that they touch the base of the plant. Their thickness far exceeds that of the upright frond; their vascular bundles lie, not in one, but in two planes parallel to the surfaces of the frond. These bundles form two many-meshed nets, one close under the upper side, and the other immediately above the lower side of the frond; the two net-works are united in many places by frequent ramifications which pass through the mass of the frond in a transverse direction.

When the plant has attained a certain amount of vigour, erect fronds are again formed, which hang over gracefully, and exhibit slightly spreading forks upon which sporangia sometimes appear. After six or eight such erect fronds have been produced, a pair of simple fronds is developed, one on the right and the other on the left of the stem. These latter fronds curve downwards. All the fronds, as well the thick flat recurved ones as also those which are slender and erect, are arranged accurately in two lines; this is seen clearly by cutting through the fronds as far back as the primary place of attachment. The direction of the frond-arrangement, judged by reference to the mode of succession of two neighbouring flat fronds, is sometimes to the right and sometimes to the left. A bud is usually formed deep down on the hinder side of the stipes of each of the erect fronds. This bud, when laid bare by the removal of the flat frond which forms a thick covering over it, becomes developed into an independent plant.

It is not difficult to conjecture the part which the thick recurved fronds play in the economy of the plant. They prevent the drying up of the place of growth. The thick covering which they form causes that portion of the bark of the trunk of the tree upon which the fern grows, to be retentive of moisture. Those species of the same genus whose fronds spread over the surface of the ground,—thus

forming a wide covering over the places of attachment of the older fronds and the ground beneath as in *Platycerium grande*,—are entirely devoid of the irregularly-shaped, fleshy, recurved frond.

The vascular bundles of the horizontal stem are arranged in a simple circle (Pl. XXXIV, figs. 8, 9); they form on the upper side a polygonal net, and on the under side a net with very narrow, parallel meshes. The arrangement of the meshes in both nets is shown in Pl. XXXIV, figs. 10, 11. The vascular bundles pass to the fronds from the angles of the meshes of the upper side. These bundles anastomose frequently in the cortical layer of the upper side of the stem. The vascular bundles of the roots originate at the upper and lower terminal points of the narrow meshes of the under side of the stem, the roots themselves being arranged in transverse rows. Roots very frequently penetrate into the substance of the decayed flat fronds, where they ramify considerably.

The cortical layer of cellular tissue which surrounds the central vascular bundle of the root, exhibits an anatomical peculiarity, having a remarkable analogy with what is seen in the epiphytal Orchids and the Aroideæ. The walls of its cells, which become brown at an early period, are thickened by a net-work of filaments. Narrow flat depressions are seen between the very delicate threads of the net (Pl. XXXIV, figs. 12, 12^b). The outermost cellular layer of the root of Platycerium, from which rootlets are emitted, has the depressions, but not the reticulate threads.

The apical cell of the end of the stem of *Platycerium alcicorne* is two-edged, having the form of a strongly-compressed cone. The arrangement of the surrounding cells discloses the fact that the multiplication of the cells of the terminal bud is brought about by the continuously repeated formation in the cell of the first degree of septa inclined in two opposite directions. A parabolical line drawn through the middle point of the places of insertion of all the younger fronds, cuts the upper surface of the apical cell of the stem, not in its shortest but in its longest diameter. The top cells of the young fronds have their edges, and not their surfaces, turned towards the ends of the stem, whose apical

cell turns its own edges towards them. These facts are directly contrary to what occurs in *Pteris aquilina*, but on the other hand they agree with what takes place in the Polypodieæ.

*Marattia Cicutæfolia.**—The flat terminal bud of this fern exhibits, when viewed from above, a three-sided apical cell as in *Aspidium filix-mas*. Longitudinal sections show a very oblique arrangement of the side walls of the apical cell and of the neighbouring cells. The rudiments of the young fronds surround the flat conical end of the stem in a spiral. The latest formed have the appearance of sharply conical protuberances of cellular tissue flattened in front, hardly distinguishable from the first rudiments of the fronds of the larger Polypodiaceæ.

In consequence of its increased longitudinal growth the top of the young frond bends over in front. During this process the stipula makes its appearance, in the first instance at the fore surface of the young frond, in the shape of a transverse protuberance (Pl. XXXIII, fig. 11). Shortly afterwards a membranous cellular mass grows in a forward direction out of each of the lateral margins of the rudiments of the frond. Those surfaces of the two cellular masses which are turned towards the protuberance of the fore-side, amalgamate with the side margins of the latter (Pl. XXXIII, figs. 11, 12). The fore margins of the two lateral lobes of the stipula remain free. In consequence of their rapid further development they almost entirely envelope the younger portions of the stem-bud. In the mean time the upper margins of the two lateral portions of the stipula grow rapidly and vigorously upwards and back-

* De Vriese and Hartings Monograph of the Marattiaceæ (Leyde et Dusseldorf, 1853, pp. 49 and 51) contains statements as to the development of the fronds of the Marattiaceæ, which, if correct, show that the process is very peculiar. It is there said, "The formation of each frond is preceded by that of its Perula. . . . It covers even the younger fronds partially. . . . The cellular protuberance, in the form of which the younger frond makes its appearance laterally near the terminal bud, consists in Angiopteris originally of cells of equal size, and of equal capacity for multiplication. The outer cells grow and multiply more rapidly, in consequence of which they separate from the inner ones. The former constitutes the membranous portion of the Perula, the latter that of the fronds." My observations on *Marattia cicutæfolia*, from which in this respect Angiopteris certainly does not differ, lead to entirely different conclusions.

wards. They assume a cap-like form, and laying hold of one another they envelope the apex of the rudiments of the frond, which now for the first time slowly elongates itself (Pl. XXXIII, figs. 15-19). Thus the rudimentary Perula is formed in all its parts, but nevertheless as an organic closed veil: its principal portion, viz., the two membranous lobes which enclose the involute frond, consists of two entirely distinct moieties overlapping one another and leaving a wide opening at the place where they impinge upon that part of the stipula which has originated from the fore surface of the rudiment of the frond (Pl. XXXIII, fig. 19). By further development this transverse portion of the stipula becomes divided at the upper margin into two cellular surfaces, one of which is bent backwards over the involute special frond, the other forwards over the rudiments of the younger fronds. By further advance in growth all the parts of the stipula, especially the basal portions, are developed to a great degree, so as to form a tissue of considerable extent, of a dark red colour on the outside and rose red within, and traversed by an intricate complication of numerous vascular bundles and passages containing gummy matter. The cells of this tissue abound with large starch-grains. Even now, however, no amalgamation takes place anywhere between the hitherto distinct portions of the stipula.

The development of the scales and roots of Marattia differs in no material respect from that of the Polypodiaceæ. The root-cell of the first degree appears three-sided both in a longitudinal and in a transverse section of the root.

It is generally known amongst gardeners that fragments of the fleshy adventitious fronds of the Marattiaceæ can be used to produce new individuals. In *Marattia cicutæfolia* this mode of reproduction may be practised with exceeding facility. The stipules, even of the most slender fronds, of specimens grown in the same manner only a few months previously, may be employed for the experiment. If these stipules be cut into pieces about half a square inch in size, and simply placed in a stoppered bottle, adventitious buds, produced at some of the numerous vascular bundles, will be seen in ten or twelve weeks to break through the bark of

the fragments of the stipules. The first fronds of these shoots have no lamina; they are entirely stipulæform.

Development of the fruit and spores. — Although much variety exists in the process of formation of those organs of ferns which surround and cover the sori, nevertheless the development of the capsules of the Polypodiaceæ exhibits, as far as present observations extend, a marked uniformity. At the place of attachment of the sorus the rudiments of the capsules are developed (contemporaneously with the appearance of the indusium where the latter is present), under the form of short multicellular hairs. The terminal cell of each swells to a globular form, and, by the effect of a series of cell-divisions, assumes the form of a body consisting of a single central cell and a peripheral cellular layer. The central cell is the primary mother-cell of the spores. By division in all three directions of space it is transformed into a globular mass of polyhedral cells—the spore-mother-cells—the walls of which become somewhat thickened. Whilst the internal cavity of the young sporangium becomes enlarged by the expansion of the peripheral layer, the walls of the spore-mother-cells swell, and the latter become disconnected, and assume a globular form. They then divide into four special-mother-cells, which in certain species are situated at the angles of a tetrahedron, in others are arranged in a decussate manner. A spore is formed in each of these special mother-cells. The membrane of the primary mother-cell is still existent at the time of the commencement of the individualization of the spore-mother-cells, and can be detached from the peripheral cellular layer.* This development of the capsule has been observed by Schacht,

* Schacht, 'Bot. Zeit.,' 1849, figs. 6, 7. The membrane of the primary mother-cell, like those of the mother-cells, is somewhat distended; the latter appear to be suspended freely in the former. Schacht was thus led to assume that the mother-cells originated by free cell-formation in the primary mother-cell (l. c., p. 544). Schacht's statement that the nucleus of each primary mother-cell separates by division into four secondary nuclei, is not confirmed by the observations which I have made upon *Asplenium filix-femina* and *Cystopteris fragilis*. In the former I found at first two secondary nuclei in the place of the primary one, and afterwards four tertiary ones in the place of the secondary ones. It appeared to me that here also the dissolution of the primary nucleus of the mother-cell preceded the formation of the nuclei in daughter-cells.

in *Pteris serrulata*, *Aspleninum Petrariæ*, and *Scolopendrium officinarum*; and by myself in *Aspl. filix-femina*, and *Cystopteris fragilis*. H. v. Mohl, in 1833, described the development of the spores in special-mother-cells (four being contained in each mother-cell), whose membranes possess a remarkable power of distension (see 'Flora,' 1833, B. i; 'Vermischte Schriften,' p. 69). In the families of ferns other than the Polypodiaceæ, few observations have been made. I may remark here, that I have clearly seen a single central cell in very young sporangia of *Osmunda regalis*. In this respect, therefore, ferns seem to agree with the rest of the vascular cryptogams, viz., that a single cell situated in the interior of the young sporangium represents the primary mother-cell of all the spores.

Historical Review.—The reproduction of ferns by means of spores was first pointed out by Morison, who states ('Historia plantarum,' Oxford, 1699, iii, p. 55) that after sowing the spores of *Scolopendrium officinarum* upon moist ground in the shade, he obtained in the following year numberless little plants of the same species, with delicate and at first roundish leaves. Ehrhart first made known with certainty that the production of the perfect fern is preceded by the development of a deeply two-lobed leaf-like body, upon the under side of which, between the indentations and the hinder end, the perfect fern is attached ('Beiträge,' iii, Hanover, 1788, p. 75). For the first accurate microscopical investigations of the germination of fern-spores we are indebted to Kaulfuss, who clearly and accurately described the rupture of the outer spore-membrane, the protrusion of the inner one, and the development of the prothallium ('Das Wesen der Farrn-kraüter,' Halle, 1827, p. 61). The sexual organs of the prothallium entirely escaped his observation, as well as the enclosure of the young embryo in the tissue of the prothallium. The discovery of this fact is due to Bischoff ('Handb. botan. Terminologie,' b. ii, Nürnberg, 1842, p. 640), who states that a wart-like excrescence originates on the back of the prothallium underneath its indentation, and that out of this excrescence the first frond breaks forth in an upward

direction and the first root downwards, the latter being surrounded at its base by the ruptured membrane of the cellular protuberance, as by a sheath. Upon the plate explanatory of this process (l. c., t. 41, fig. 2385) an empty antheridium is shown upon the prothallium, without however any mention of this organ being made in the text. Two years afterwards Nägeli published the discovery of the antheridia and spermatozoa of the ferns ('Zeitschr. f. wissensch. Bot.,' Zurich, 1844, p. 168). He describes the origin of the antheridium, of the mother-cells of the spermatozoa, and of the spermatozoa themselves, essentially in conformity with the account given in the preceding pages; he brings clearly forward the similarity of the antheridia of the ferns with those of the Muscineæ and asserts that the antheridia are very probably the male organs, although it remained almost inexplicable to him in what relation they could stand to the impregnation, which he considered only to affect the spores. It is beyond question that Nägeli also observed the archegonia of ferns, but misunderstood them: they are the organs which he describes and figures (l. c., p. 171, t. iv, fig. 11—15) as many-jointed antheridia. The real nature of the archegonia was first correctly ascertained by Count Leszyc-Suminski ('Zur Entwickelungs-geschichte der Farrn-kräuter,' Berlin, 1848). He pointed out (l. c., p. 13) that the rudiments of the frond-bearing plant always appeared on the underside of one of the archegonia, inside a cavity sunk in the tissue of the cushion of the prothallium, and he assumed that in order to excite the development of this embryo, the entrance of one or more of the spermatozoa was necessary. He observed the cilia of the spermatozoa, but did not figure them quite accurately. Suminski's correct conclusions were arrived at by observations which were to a great extent erroneous. He believed that the archegonium in its youngest condition, and before its neck protruded above the surface of the prothallium, was open at its apex; and that at this period the entrance of the spermatozoon into the central cell took place. He called the latter the cavity of the germinal vesicle and its nucleus the germinal vesicle itself. He considered that the longitudinal development

of the neck of the archegonium and the closing of its mouth did not take place until after the entrance of the spermatozoa. According to his view one of those spermatozoa which had first effected an entrance into the archegonium then penetrated with its pointed end into the embryo-sac which in the mean time had become multicellular; the pointed end then became swollen and converted into a spherical cell which gradually displaced the tissue of the embryo-sac, formed new cells in its interior, and thus constituted the embryo. He thought that the spermatozoa which had entered the archegonium at an early period, and which had not aided in the formation of the embryo but had reached the canal of the neck, were there transformed into the worm-shaped masses which I have pointed out as the product of the transformation of the cells of the axile string of the neck of the archegonium. From the erroneous notion entertained by Suminski as to the development of the archegonium, it is quite clear that his observations upon the entrance of the spermatozoa into the central cell must be founded on a misconception, and that he never really saw the spermatozoa enter the archegonium at all. His idea of the formation of an endosperm in the embryo-sac is founded upon an incorrect arrangement of the different stages of development which he observed; the body which he designates as endosperm, as "multicellular parenchyma filling the embryo-sac," is in fact the young embryo. L. Suminski first observed the cilia of the fore-end of the spermatozoa, but did not draw them quite correctly (l. c., t. ii, figs. 20, 21). Thuret gave the first accurate figures of them ('Ann. d. Sc. Nat.,' 3rd ser., vol. xi, p. 5). A succession of works by other observers followed quickly upon the publication of Leszyc-Suminski's treatise. First came Wigand in the 'Bot. Zeitung,' for 1849. He disputed most of the statements of his predecessor, even those which were quite accurate, such as the constant occurrence of the cavity (of the central cell) beneath the free portion of the archegonium (l. c., p. 78); the regularity of the pressure of the neck of the archegonium upon that layer of the tissue of the prothallium which covers the enclosed young embryo (l. c., p. 77, 106);

the normal concealment of the young embryo in the tissue of the prothallium (l. c., p. 106), and even the possibility of the access of the spermatozoa to the archegonia (l. c., p. 78). On the other hand in the 'Bot. Zeitung,' for 1849, p. 796, I have given my opinion confirmatory of the principal point in L. Suminski's statements, viz., the regular development of a young plant in the interior of one of the organs called Ovula by L. Suminski. I added that the parting asunder of the four longitudinal rows of cells which form the neck of the archegonium, is the cause of the opening of the passage which leads to the large cell at the bottom of the female organ, and that Suminski's "Endosperm" is in fact the young plant. At the same time I called attention to the facts that the antheridia and archegonia of mosses exhibit in their structure the most striking similarity to the like organs in ferns, and that the development of the embryo of the vascular cryptogams coincides in its principal features with that of the fruit in mosses, inasmuch as in both those large groups of plants the fruit is not developed in a continuous course of vegetation from the germination of the spore, but in both families the development suffers a discontinuance; in an organ which has essentially the same structure in both families, a cell originates, in which, after exposure to the access of spermatozoa, an independent cellular body is formed, morphologically distinct from the mother-plant, upon which the mosses are dependent for the development of their fruit only, but to which the ferns owe by far the most important part of their vegetative growth. In a work which appeared shortly afterwards ('Linnæa,' B. xxii, 1850, p. 753) Schacht also pointed out that the archegonia of ferns are formed just like those of mosses; that they are at first closed, and are furnished at the base with a cavity sunk in the tissue of the prothallium, which cavity is in communication with the canal which traverses the neck of the organ; that in the interior of the cavity, and probably inside a cell clothing the cavity, the embryo is formed. Like myself, Schacht considers that the filiform mucilaginous bodies inside the closed canal, which L. Suminski looked upon as transformed spermatozoa, are the products of the transfor-

mation of the primary contents of the canal, and that Suminski's endosperm is the embryo (l. c. p. 780). On the other hand V. Mercklin's conclusion from the examination of the same object ('Beobachtungen am Prothallium der Farrn-kräuter,' Petersburg, 1850) was more in favour of Suminski's views. V. Mercklin also thought that the young archegonia were open, and believed that he had seen the entrance of spermatozoa into such young archegonia, and he assumed that it was not until a subsequent period that the apex of the neck of the archegonium became closed (l. c. p. 46). On the other hand he observed correctly the bursting of the apex of the archegonium after its complete formation (l. c. p. 33) as well as the presence of a globular cell in the central cell (which like Schacht and Suminski he took to be an intercellular space) before the bursting of the latter (l. c. p. 31). To V. Mercklin also is due the merit of the first reliable observations of the entrance of the motile spermatozoa into the mouth of the neck of an opened archegonium (l. c. p. 46 in *Asplenium Serra*). Mettenius ('Beiträge zur Botanik,' Frankfurt 1850, p. 18) arrived at the same results as Schacht and myself. He first pointed out that the development of an archegonium from a cell of the prothallium, commences with the division of this cell into two cells lying underneath one another (l. c. p. 19).

In my 'Vergleichende Untersuchungen' Leipzig 1851, p. 81, I added to the account which I had published two years before. The principal points in the literature of the sexual reproduction of ferns received a further confirmation from a paper of Henfrey's in the 'Transactions of the Linnean Society,' vol. xxi, p. 117, 1852. In 1851 I was under the impression that the germinal vesicle of ferns originated by renewed cell-formation round the primary nucleus of the central cell, an error which I corrected in 1854 ('Sitzungsberichte K. Sächs. Gesellsch. d. Wissenschaft,' Math. Phys. Cl. 1854, p. 54) when reviewing my first observations on the motile spermatozoa in the central cell of the archegonium. In a publication which appeared soon afterwards, Wigand retracted his previous contradictions of the statements of other observers, (Botanische Untersuchungen, Braunschweig, 1854, p. 151) so that

botanists are now unanimous upon all the essential points of the question.

The anatomy of the stems of ferns (the course of whose vascular bundles had been supposed to be very similar to that of the monocotyledons) was first clearly explained by H. v. Mohl (de structurâ caulic. filic. arbor. in v. Martius' Icon. plant. cryptog. Brasil. Munchen 1835; translated in H. v. Mohl's 'Vermischte Schriften,' p. 108). He pointed out that the closed vascular bundles (which do not increase in thickness after they are first formed) in tree ferns as well as in the herbaceous species form a hollow cylindrical net concentric with the periphery of the stem, whose meshes, in the species with crowded fronds (*Aspl. filix-mas* for instance), are arranged with the greatest regularity in the following manner, that is to say; from the place where each frond is attached to the cylinder, two bundles pass to the bases of the two next higher fronds, and two to the bases of the two next lower ones. This regularity in the relation between the anastomoses of the vascular bundles and the places of insertion of the fronds, does not occur in the species with distant fronds, such as *Polypodium aureum*. The difference between the tree-ferns and the herbaceous species is immaterial, depending upon the breadth of the vascular bundle, and the development of the sheaths of the latter out of woody prosenchyma. At the place where a vascular bundle passes into a frond an *entire* bundle is never found to bend itself outwards for that purpose, as is almost always the case in phænogams, but small ramifications only are sent off into the fronds.* Later observations have not yielded any additional results of importance.

Brogniart first made known that the ramification of the stems of ferns is caused exclusively by bifurcation of the extremity ('Histoire des vegetaux Fossiles,' ii, p. 30), an opinion which has been supported by Stenzel ('Jahresb. Schles. Ges.,' 1857, p. 85), and by myself.† On the other

* Unger's notion of the ferns and their allies as "*Plantæ acrobryæ*" is founded upon this important peculiarity ('Unger Bau und Wachsthum der Dikotyledonen-stamen,' Petersburg, 1840; 'Anat. und Physiol. d. Pfl.,' 1850, p. 225).

† My observations on this subject which are given in the preceding pages were first published in the Transactions of the Royal Society of Sciences of Saxony, vol. v, p. 60. 1857.

hand, Karsten ('Vegetationsorgane der Palmen,' Berlin, 1847, p. 125), called attention to the definite relation which so often occurs between the ramifications of fern-stems and the insertion of their leaves; and Mettenius lately endeavoured ('Abhandl. K. Sachs. Ges. d. Wiss.,' vol. vii,) to show that no essential difference exists between the mode of ramification of ferns and of the vascular cryptogams generally, and that of phænogamous plants, inasmuch as the ramification of ferns owes its origin to the development of lateral buds, which are normally situated in a definite position with regard to the bases of the leaves. Mettenius draws his conclusions from a number of species of Trichomanes, whose lateral buds he considered to be undoubtedly situated in the axils of the fronds. He finds even in Hymenophyllum instances of the transition between axillary buds and buds springing from the fore side of the stipes. With these he classes the Davallieæ, which exhibit transitions from axillary buds to buds which originate in front of and underneath the axil. Mettenius finds the buds of *Platycerium alcicorne* and of many other species behind and underneath the insertion of the fronds, and in *Polypodium vulgare* (amongst others,) he finds the bud so far removed from the point of insertion of its own proper frond, that it appears to be opposite the next older one. Mettenius considers these lateral buds to be of the same nature as those found on the stipes of *Pteris aquilina* and *Aspidium filix-mas*, which I look upon as adventitious buds distinct from the true ramifications of the stem. He adopts Karsten's view, that in Dicksonia, in consequence of a bud of this nature being developed at an early period before the development of the frond belonging to it, the frond which originally belonged to the stem is withdrawn from the latter, and transferred to the apparently dichotomous ramification of the principal stem. Mettenius also agrees with Karsten as to the mode of branching of the stem of *Pteris aquilina*.

If the object of this conception is to point out the essential agreement between the ramification of the vascular cryptogams and the axile position of the lateral branches of phænogams, it may be objected that the agree-

ment in question assumes a very different aspect, if the view suggested by Pringsheim ('Bot. Zeit.,' 1853, p. 609), and supported by Irmisch ('Bot. Zeit.,' 1858, p. 492) be adopted. According to this view (which I consider correct), all normal ramification rests upon bifurcation of the end of the stem above the youngest leaf of the bud, the result of which usually is, that one fork of the branch developes itself more vigorously than the other, and forms the prolongation of the principal axis, whilst the other which is less strongly developed and is displaced sideways, forms a lateral branch. It is hardly necessary to remark that the existence of a definite relation between the positions of the branches and the leaves is entirely reconcileable with this view. No supporter of it has denied the fact. In phænogams the less-developed branch,—which, in consequence of its inferiority of development becomes a lateral branch of the more vigorously developed one,—is usually inserted in the axil of the next lower leaf, but this circumstance is of little importance, inasmuch as no causal connexion is anywhere proved to exist, or as far as we know even suspected, between the anatomical relations of the axil of the leaf and the insertion of the lateral branch. Nothing is more certain than that the rudiment of the lateral branch in all cases hitherto examined is formed immediately after the commencement of the formation of the phyllophore, and that the next higher leaf in a vertical direction is first formed at a much later period. The essential difference between the existing opinions relates therefore only to the question whether the dichotomous ramification of fern-stems and the formation of buds at the base of the stipes of ferns are processes of a similar nature; whether both stand in the same relation to the principal axis as the axillary buds of phænogams. Observation gives immediately a negative answer. The adventitious buds which are situated upon the back of the stipes of *Aspidium filix-mas*, as well as those which are inserted lower down in *Pteris aquilina* and Struthiopteris, are not formed until the frond has reached a high degree of development, a fact quite at variance with the mode of production of the axile buds of monocotyledonous or dicoty-

ledonous plants, and of the forked branches of ferns. I should not adopt the definition given by Mettenius of lateral and adventitious buds. I should call those buds *lateral* buds, which originate from the naked apex of the stem above the insertion of the youngest leaf, and are thus formed by bifurcation of the end of the stem, whilst owing to their inferiority of development they are pushed aside by the other division of the forked end of the stem. I should call those buds *adventitious* which make their appearance underneath the insertion of the youngest appendicular organ, whether on the outer surface or in the interior of the tissue. The term Dichotomy might then be applied to the cases of equal development of the two ends of the fork of the stem. These definitions leave the doctrine of ramification as established by Schimper untouched. The fact, that in phænogams that branch of the end of the stems which is situated in the axil of the next lower leaf is usually less vigorously developed than the other one, justifies the assumption, that the cases in which the former is more vigorously developed than the latter must be looked upon as special instances of ramification. If a comparison be made between the adventitious buds of *Aspidium filix-mas* (which are of frequent occurrence), and the early conditions of the bifurcations of the apex of the stem of the same species (which are of rare occurrence), or between the bifurcations of the apex of the stem of *Asplenium filix-femina* (which are of frequent occurrence), and the adventitious buds at the base of the stipes of the latter plant (which are of very rare occurrence), it will be self-evident that in these instances the two things are quite as distinct as (for example) the bifurcations of the end of the stem of *Metzgeria furcata*, and the adventitious shoots which are developed from the marginal cells of the flat stem of the latter plant.

Upon examining the bifurcations of *Asplenium filix-femina* whilst in a very early stage of development, after having removed all the older fronds and scales, I found that the two ends of the axis, when viewed from above, presented the appearance of conical protuberances of equal size, each surrounded by the rudiments of only three fronds.

The arrangement of the fronds in both was antidromal, and in one of them always passed by degrees into that of the older undivided axis, whilst the frond-arrangement of the adventitious shoots of *Aspidium filix-mas* is usually homodromous with that of the principal stem, and rarely antidromous to it.

With regard to *Pteris aquilina* the inadmissibility of the views of Karsten and Mettenius is still more manifest. I have seen stems of *Pteris aquilina* with naked frondless unbranched ends of considerable length, whose youngest branch disclosed no rudiment of a frond. This was the case (amongst many other instances) throughout a length of eight inches in a portion of the end of a stem, and throughout a length of $2\frac{1}{5}$ inches in the youngest branch. This is proof of undoubted bifurcation. The supposition of Mettenius would also require that (when the first frond of the sub-axis is inserted on the side turned towards the principal axis) a bud inserted on the hinder edge of the stipes should, by its early development, push away the frond from the principal axis to which it belongs. It would follow also that the front surface of its lamina must be turned towards the latter, or in other words its stipes must exhibit a tension of 180°. Neither of these two circumstances occurs.

Finally a real difference exists between the internal structure of the forked branches of the stem and that of the place of junction of the principal stem with the buds which I have considered as adventitious and seated on the stipes. The former exhibit throughout their entire length the peculiar structure of the stem. Their two axile vascular bundles, and the sheaths of the latter, are united immediately with the corresponding portions of the tissue of the principal axis. The tissue on the other hand which lies between the principal axis and the place of origin of an adventitious bud, exhibits the characteristic arrangement of the vascular bundles of the stipes.

CHAPTER VIII.

EQUISETACEÆ.

Equisetum arvense, pratense, variegatum, hyemale, palustre, limosum.

THE growing end of the stem of each shoot of the Equisetaceæ consists of a blunt conical mass of cellular tissue, and projects considerably beyond the place of origin of the youngest leaf. The latter encloses the terminal bud in the form of an annular cushion of uniform height. The next youngest leaves are immediately underneath it, and closely packed together. Their upper margins already exhibit the first indications of the pointed lobes, into which the sheaths which surround the base of each joint of the stem are prolonged (Pl. XXXV, figs. 6, 7).

The longitudinal growth of the stem* is produced by repeated division of the large apical cell of the terminal bud, which cell is three sided beneath, and sharply pyramidal. The division takes place by means of septa which, following a left-handed spiral direction, are successively parallel to each one of the lateral surfaces (Pl. XXXV, figs. 3, 4). The cells of the second degree thus formed divide immediately twice over, by means of vertical septa which make acute angles with the lateral surfaces of the cell and pass to its free outer surface in a gentle curve concave towards these lateral surfaces. That septum is usually formed first which is seated upon the older side-wall of the cell

* The cell-succession in the end of the stem of Equisetum was first correctly described by Cramer (Nageli and Cramer, 'Pflanzen-physiol. Untersuch.,' Heft 4, Zurich). I had previously erroneously considered the form of the apical cell to be that of a wedge. I have mentioned the cause of this erroneous assumption in speaking of the cell-succession in the growing end of the stem in Sphagnum.

(Pl. XXXV, fig. 3). The middle one of the three cells which are produced in the interior of the cell of the second degree (all of which lie in one plane) is the only one which reaches to the middle point of the stem. It divides into an inner and an outer cell by means of a longitudinal septum almost parallel to the chord of the curved free outer surface (Pl. XXXV, fig. 5). Both are divided by a transverse septum, the outer one usually before the inner one (Pl. XXXV, fig. 2). In the former this septum is parallel to the upper and under surface of the cell; in the latter it is usually horizontal, and at right angles to the longitudinal axis of the shoot (Pl. XXXV, fig. 1). The stem forthwith increases in thickness by repeated division of the cells of the circumference by means of septa parallel to the free outer wall. In very vigorous shoots, as for example in the autumn shoots of *Equisetum limosum*, the like division occurs several times in the cells of the next inner layer also (Pl. XXXV, fig. 1). In such buds the cells of the circumference usually divide once more by transverse septa close above the place of origin of the youngest leaf. During the increase of the stem in thickness the number of the cells of its circumference increases continually by the division of these cells by means of septa radial to the longitudinal axis of the shoot or at least only slightly diverging from the radial position. At first, in the upper part of the conical cellular mass, this division alternates very regularly with division by longitudinal septa parallel to the outer wall of the cells; lower down, where the stem becomes thicker, division by a radial septum does not occur until after several divisions by septa parallel to the axis of the stem. The mass of the end of the stem which lies above the youngest leaf, and the number of the cells of its longitudinal axis and of its circumference are very different in different species and even in the shoots of the same plant; they vary with the vigour of the shoots. By the early occurrence of transverse division in the cells produced by the multiplication of a cell of the second degree, the ladder-like interweaving of the cells of the two longitudinal halves of the stem is equalised at an early period. In those cases in which this division does not extend into the cells adjoin-

ing the axis of the stem, it occurs at least once in the cells of the circumference. On the upper surface of the stem therefore an extremely regular circular girdle of cells is to be distinguished. At a definite distance from the apex of the terminal bud all its outer cells which lie at the same altitude (a girdle of cells enclosing the end of the stem) divide contemporaneously by a septum inclined to the horizon (Pl. XXXV, fig. 2). In the outer (the upper) of the two cells thus formed, a division takes place by a septum inclined in an opposite direction. Thus an annular wall of uniform height and embracing the terminal bud is raised a little beneath the apex of the latter: this is the first rudiment of the youngest leaf. All the cells of its free upper edge continue to divide by alternately inclined septa (Pl. XXXV, fig. 1). The leaf at first grows upwards in the form of a cylindrical sheath of uniform height enclosing the terminal bud (Pl. XXXV, figs. 6, 7).

The place of origin of the youngest leaf, the girdle of its mother-cells, is close above the place of attachment of the next younger leaf. The leaf very soon after its production begins to increase in thickness, the cells of its base,—those of the under surface exclusively (Pl. XXXV, fig. 1),—dividing repeatedly by septa parallel to this surface. This cell-multiplication progresses slowly from the base of the leaf to its apex, and finally ceases at a considerable distance beneath the latter. The outer (or lower) ones of the cells thus formed, divide by transverse septa (septa parallel to the ideal longitudinal axis of the leaf) the division being more frequent in proportion as the shoot is destined for more vigorous development. The great excess in the number of the cells of the under surface of the leaf over that of the upper, causes the free upper edge of the leaf to bend inwards. By the vigorous multiplication of the lower portion of the outer surface of the leaf, the base of the leaf is soon transformed into numerous layers of cells, parallel to the longitudinal axis of the shoot, and representing the outer circumference of the stem (Pl. XXXVI, fig. 1). The subsequent increase in length and thickness of the joints of the stem depends upon the increase in

length and breadth of this cellular mass which has arisen from the development of the basal portion of the leaf-rudiment. The central cellular cylinder of the stem which has arisen immediately from the terminal bud becomes exclusively pith.* In the mean time by longitudinal division of the cells of the leaf in a direction radial to the axis of the stem—a division which occurs as well in the cells of the under part which represents the outer layer of the stem, as also in the free sheath-shaped upper portion—the number of the cells of the circumference of the stem-joint and of the hollow cylindrical leaf continually increases.

Shortly after the first appearance of the leaf there may be observed an inequality in the activity of the growth of its free upper edge. In the first place, at four points of the leaf, one of the cells is about one step in advance of all the rest in the process of division, which division takes place by septa turned alternately towards and away from the longitudinal axis of the stem (Pl. XXXV, fig. 8). The neighbouring cells on the right and left are about one step in arrear: the cells adjoining the latter cells remain one step further in arrear. Four short blunt points are thus produced, placed in pairs opposite to one another upon the upper edge of the sheath-like leaf. The multiplication of the cells of the circumference of the free upper edge of the leaf is produced exclusively by the division of the apical cells of these points by means of longitudinal septa (Pl. XXXV, fig. 8).† This division of the apical cells of the tip of the leaf by septa radial to the circumference of the leaf-sheath is often repeated at certain stages of the growth of the leaf, and increases the breadth of the tip more and more. Shortly afterwards the widened apex of the tip of the leaf exhibits the first indication of a rapid bifurcation (Pl. XXXV, fig. 9). Thus with the age of the leaf the number of the teeth of its edge increases; in

* From an opposite point of view, viz., the comparison of finished stages of development, Spring arrives at the same conclusion for larger divisions of the vegetable kingdom ('Monographie des Lycopodiacées, extraite des Memoires de l'Academie Royale de Belgique,' Bruxelles, 1849).

† This mode of growth of the tip of the leaf brings strongly to mind that of the shoots of Riccia, &c.

strong shoots of *Equisetum limosum* this increase takes place with great regularity according to the progression 1 . . 4 7 . . 8 . . 9 . . 10 . . 11 and so on to 20 (Pl. XXXV, fig. 7). At about the fourth or fifth leaf (reckoning backwards from the uppermost youngest leaf) there occurs a very remarkable longitudinal elongation of the cells of the apices of the tip of the leaf. Even after its commencement, the multiplication of the cells of the base of the leaf in a longitudinal direction by means of septa at right angles to the axis of the stem continues for some length of time.

The relation of the outer cellular layers of the stem (which are produced by the development of the outer side of the base of the leaf-rudiment) to the central pith cylinder, which corresponds with the cells of the free portion of the terminal bud, is very different in the different forms of shoots. In the few vigorous shoots which are usually developed in autumn by the subterranean internodes of *Equisetum palustre* and *pratense*, and in a still more marked manner in *Equisetum limosum* and *hyemale*, the distinction between the pith and the outer layer of the stem is visible at a very early period: the cells of the latter even in the youngest joints of the stem often divide repeatedly in a longitudinal direction, whilst the multiplication of the pith cells is quite at a stand-still. On the other hand this distinction occurs at a comparatively later period, and is not nearly so well defined, in the delicate shoots which break forth from the bases of the leaves high up on the stem, especially in the thin shoots of the second, third, or fourth order of *Equisetum pratense, arvense* and *limosum*, or even in the shoots of the first order of *Equisetum variegatum*. The following table shows the number, in a longitudinal direction, of the cells of the pith (*a*) and those of the outer layers (*b*).

	In the 1st internode.		In the 2nd.		In the 3rd.		In the 4th.		In the 5th.		In the 6th.		In the 13th.	
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
In *Equisetum palustre* (a vigorous shoot)	4	4	4	4	4	7	4	8	4	8	...	...	...	...
The same species, a very delicate shoot	4	5	4	5	7	9	9	12*	...	...	...	...	...	...
Eq. limosum (a shoot formed at the end of May)	4	4	8	8	8	10	8	17	...	...	...	...	...	...
Eq. limosum (a vigorous autumn shoot)	4	4	4	6	4	7	4	7	4	10	4	10	8	13†
Eq. pratense (a vigorous autumn shoot)	4	4	4	6	4	6	4	7	4	7	...	...	...	...
Eq. variegatum (a delicate shoot)	3	3	7	7	7	7	7	13	...	...	...	...	...	...
The number of cells of the transverse diameter in a vigorous autumn shoot of *Eq. limosum* amounted to	22	...	32	...	40	...	48	...	58	...	...	...	...	...
In a delicate shoot of *Eq. variegatum* to	5	...	8	...	9	...	12	...	12	...	12	...	...	...

This comparison appears at the first glance to be quite at variance with the common notion that the cells of the stem are multiplied in a longitudinal direction only at the apex of the organ. This opinion is untenable in any extended sense. As far as observations go there are no plants, from the mosses upwards, in which the cells of the stem are multiplied in a longitudinal direction exclusively by division of the terminal cell. Generally the division of the daughter-cells of the cells of the second degree by septa at right angles to the longitudinal axis, plays an important part in the production of longitudinal growth. On a more accurate examination, however, the above table, shows that there is a special tendency to multiplication in the cells of those parts of the leaves which have been already some time formed. It is only the cells of the cortical layers (which my figure Pl. XXXV, fig. 1, shows clearly to have been produced by the multiplication of the cells of the leaf-rudiment) which exhibit the long-continuous longitudinal

* Those of the epidermis 14. This fourth internode exhibited the first indications of annular vessels, 5—6 rings in each of the cells of a longitudinal row adjoining the pith.

† A trace of annular vessels was first visible in the 15th internode.

multiplication extending in many cases even beyond the twelfth internode. In the cells of the pith only a single transverse division occurs. From the fact that the thickness of the shoot is in such manifest connexion with the period of the occurrence of the transverse division of the pith-cells, it may perhaps be concluded that the immediate operation of the outer air upon the tissue of the growing stem has an especial effect in promoting transverse division in the cells.

The formation of the epidermis of the young stem-joint is contemporaneous with its longitudinal extension, with its appearance above ground, and with the formation of numerous chlorophyll-bodies in the cells of its circumference. All the cells of the outer surface divide twice by transverse septa, then by longitudinal septa, and lastly by septa parallel to the outer surface. A double layer of cells is thus produced, enclosing the circumference of the stem, the cells being one-eighth the size and eight times as numerous as those of the next inner layer. The outermost are transformed into the epidermis; every second cell of the epidermis of the above-ground shoots becomes the mother-cell of two stomatal cells; these as well as the tabular cells of the epidermis exhibit upon the outer surface very regular projections the form of which is constant for each species (Pl. XXXVI, fig. 2). These projections contain more siliceous matter than any other part of the stem.

The differentiation of the vascular bundles from the surrounding tissue commences a short time before the formation of the epidermis. The first commencement of the vascular bundle consists in the appearance of annular fibres in a vertical row of cells the position of which answers exactly to one of the tips of the next higher leaf. From five to six of these annular fibres occur in each cell (Pl. XXXV, fig. 13). A plane passing through the middle of the tip of the leaf cuts the string of cells of the stem-joint which bears the leaf, in each of which cells annular fibres are formed.

The horizontal septa which separate the ring-bearing cells from one another are very soon absorbed, and a circle of annular vessels traversing the entire length of the stem-

joint is thus produced. At the time when the annular vessel becomes continuous a multiplication commences in the neighbouring cells—those situated in front (towards the outside) and to the side—by means of vertical septa alternating with radial septa and with septa parallel to the periphery of the stem (Pl. XXXVI, fig. 1). Thus a thick string of cambial cells is produced in which more annular vessels (with much narrower rings) are shortly afterwards formed in a similar manner, and where at a much later period spiral vessels are also formed. In the developed internode this string of cells represents a closed vascular bundle.

The tips of each leaf and the corresponding vascular bundles of each stem-joint alternate with those of the next lower one. Soon after the first separation of the vascular bundle from the surrounding tissue of the stem—which separation takes place whilst the vascular bundle has still the appearance of a string of cambial cells and exhibits only a single annular vessel on its inner side—the cells of the node from the base of the vascular bundle as far as the two adjoining ones of the next lower stem-joint are transformed into short spiral cells arranged in a moniliform manner; the cells which adjoin these strings in a lateral and outward direction are transformed into a thin layer of cambial cells which at a later period also take part in the formation of vessels.

After the commencement of the formation of the vascular bundle of the stem the corresponding leaf-tip exhibits the transformation of a string of cells into a vascular bundle traversing its median longitudinal line. The first vessels which appear in the leaf are elongated, narrow, spiral vessels. The vascular bundles of the leaf attain only a slight thickness.

The distance from the middle point of the stem at which the formation of vascular bundles commences—in other words the bulk of the pith and the number of leaf-tips and the (corresponding) number of the vascular bundles of the internode which bears the leaf—is very variable according to the activity of the growth of the shoot, and according to the number of its diametral cells. In thin shoots of *Eq.*

variegatum and *palustre* the number of cells in the diameter of the pith is only 6; in vigorous shoots of *Eq. limosum* it is 40. The number of leaf-tips and vascular bundles appears not less variable; in the main shoots of *Eq. variegatum* it is 7; in *Eq. palustre* 7—10; in *Eq. pratense* 10; in *Eq. limosum* 10—20. Most striking differences in this respect are found even in the axes of different orders of one and the same shoot.

The connexion between the cells of the pith of all the indigenous (German) species of Equisetum is very soon dissolved. The numerous intercellular spaces become filled with air. The cells of the pith are soon unable to keep pace with the longitudinal growth of the periphery of the stem. All connexion between the pith-cells ceases, they are torn from one another, they become shrivelled, and in a short time disappear altogether with the exception of a flat double layer of cells in each internode which lasts as long as the stem itself. Thus there is produced in each internode a central pith-cavity covered above and filled with air, having smooth side walls and a base rough with the debris of the pith-cells. In just the same way—by the separation of a string of cells from the adjoining tissue, by the early cessation of the multiplication of these cells, and by their shrivelling and desiccation—an air-cavity is produced, in *Equisetum limosum*, around each vascular bundle; and ultimately by the decay of the central portion of the vascular bundle, a narrow air-cavity is formed in the interior of each of them.

Normally, the terminal bud of the Equisetaceæ never ramifies. There is hardly any other group of plants which exhibit such a well-defined, exclusively apical, growth. Ramification is caused solely by adventitious buds. These are produced in definite positions, viz., in the annular locus of insertion of the sheathing leaf; each adventitious bud, with rare exceptions, being seated under the angle between each two leaf-tips. The rudiment of the adventitious bud appears long before that of the vascular bundles of the same internode. In the autumn shoots of *Eq. pratense* which are developed in the following spring, a cell, situated in the defined position at the base of the

leaf (often of the third or fourth-youngest leaf), and in the second or third layer beneath the surface of the latter, becomes distinguishable from the neighbouring cells (which often already contain chlorophyll), by its increase in size, and still more by its colourless thickly mucilaginous contents. This cell often lags behind its neighbours in longitudinal growth, in consequence of which its connexion with the cells above it and at its sides is dissolved. Division soon commences in it, and is repeated in different directions in rapid succession in the terminal cell. (Pl. XXXV, figs. 11, 12). Thus a cell-multiplication is set on foot which corresponds in all respects with the preceding multiplication of the apical cell of the terminal bud. The presence of the adventitious bud is soon indicated by a protrusion of the outer surface of the stem close under the place of insertion of the leaf. Ultimately by further longitudinal growth it breaks forth from the under-side of the sheath-like leaf.

The adventitious buds of Equisetum have the peculiarity of being able, under certain circumstances, to remain long dormant, a peculiarity which they possess in common with the adventitious buds which are produced in mosses and phænogams upon the outer surface of the young stem in the axils of leaves. They often pass the greater portion of a period of vegetation in the most rudimentary condition, consisting of one or at most of a few cells. This is the case with the adventitious buds of *E. pratense, palustre,* and *limosum,* which are destined to reproduce the species. Although in spring numerous thin branches break out from the base of the leaf-sheath of the middle and upper part of the above-ground shoots, the number of which branches is usually the same as that of the leaf-tips, yet the adventitious buds of the lowest internodes—those which are buried in the earth—remain entirely dormant until late in autumn. At that time, however, one only of the buds of each of those internodes developes itself but with a strength and activity which far exceeds that of the subterranean branchlets.

Individual internodes of the lower subterranean portion of the main shoots of *Eq. arvense* become swollen, whilst

the cells of the tissue which surrounds* the circle of vascular bundles multiply vigorously. Vigorous adventitious buds are formed at the base of the rudimentary leaf of such internodes; seldom more than two in the same internode. The cellular tissue of the swollen internodes contains starch and a good deal of sugar, I believe not crystallized. The different habit of the species of Equisetum depends upon the relation of the adventitious lateral shoots to the principal shoot. In all the above-named species (*arvense, pratense, variegatum, hyemale, palustre, limosum*), the lowest leaves of those shoots which have completed their subterranean development, send out vigorous shoots destined for development in the following season, a process which brings to mind the buds which occur in the cataphyllary region of many phænogams. These shoots are the least developed in *Eq. arvense;* they are of an elongated cylindrical form, and very beautiful and vigorous in *Eq. pratense* and *limosum*. In the latter species they protrude, even in autumn, for a distance of several inches from the base of the sheathing leaves; in *Equisetum palustre* they appear at the beginning of spring; in *Eq. hyemale* at the end of April. Those of *Eq. limosum* deserve a closer investigation, not only on account of many peculiarities dependent upon habitat, but also on account of the injury produced by its abundant growth in the richest water-meadows of North Germany, where the hay is frequently uneatable from the admixture of numerous shoots of the Equisetum. As in the other species of the genus, the lower part of each shoot (unlike the portion above ground), does not die until the autumn. The epidermis of this portion of the stem assumes a beautiful red-brown colour; from one to three shoots, destined for development above ground in the following year, burst forth in an upward direction out of the hollow cylindrical leaves, whose upper portion dies and withers. The epidermis of these winter shoots is of the colour of ivory, and the tips of their leaves of a chestnut-brown. If the shoots are exposed to the light, chlorophyll is developed, even in autumn, in the cells of the circumference. Be-

* Compare Bischoff 'Kryptogamische Gewächse,' Nurnb., 1828, Heft i, p. 29.

sides these shoots others are developed here and there on individual joints of old stems: the latter have a lateral, not an upward direction; their colour in the young state is a deep citron-yellow, and their leaf-sheaths are of a deep black-brown. Unlike those first described, they are not blunt at the top, but the connivent tips of the sheathing leaves of the terminal bud form a sharp apex. These shoots are the foundation of the creeping rhizome, and sometimes attain a length of twenty feet. When they emerge from the leaf-sheaths of the mother-shoot they are of the thickness of a slender goose-quill, but afterwards by expansion of their cells, and by gradual increase in the number of the cells of the new internodes in a diametral direction, they attain from half to three-fourths of an inch in thickness. From the bases of their leaf-sheaths a few shoots are produced separated from one another by considerable intervals (by several internodes, which produce no adventitious buds), and which are destined partly for development above ground, and partly for the formation of new Rhizomes.

In those species of Equisetum which are found in damp localities away from the light, a girdle of adventitious roots is formed at each node of the stem, on a level with the septum which traverses the pith cavity, and close underneath the rudiments of the adventitious buds. They originate close underneath the bark, immediately below the lower ends of the vascular bundles of the next superior internode, and consequently meet the upper ends of the septa which separate the cortical air-cavities of the next lower internode. In the lower nodes of the vigorous autumn shoots one at least, usually two, and often three such adventitious roots are formed close to one another. At an early period the cells of that portion of the partition wall of two cortical air-cavities which leads from the adventitious roots to the convergent prolongations of the vascular bundle are transformed into a single vascular bundle traversed by numerous short spiral vessels. The origin of these thick vascular bundles, which are attached to the spreading prolongations of the vascular bundles of the internode, renders the course of the vascular bundle of the stem within the node quite indistinct; they

may have given rise to the opinion that the vascular bundles of the stem of the Equisetaceæ unite in each node to form a confused mass of tissue.*

The normal mode of cell-multiplication in the punctum vegetationis of the adventitious roots is identical with that in *Aspidium filix-mas*. The cell of the first degree, whose continuous division is the cause in the first instance of the growth of the root lies in the interior of the tissue, nearly above the apex of the root. Its form is tetrahedral. It divides by septa of which three in succession are each of them parallel to one of the three lateral surfaces, and of which the fourth forms the surface of a segment of a sphere seated upon the basal surface which is turned towards the apex of the root. In this way sets of four cells of the second degree are formed, of which the three upper, which adjoin the cell of the first degree, take part in the formation of the permanent portion of the root; the fourth, by its multiplication produces one of the hood-shaped layers of the root-cap. Soon after its formation four cells, having a quadrantal basal outline, are produced in its interior by a twice repeated division by means of vertical septa. The cells produced by the multiplication of one of the lower cells of the second degree henceforth divide only by septa perpendicular to the basal surface of the mother-cell and consequently to the next adjoining portion of the surface of the root. All the daughter-cells of such a cell of the second degree lie in one place which is curved parabolically; they form a blunt hollow cone, and the number of these cones which envelope the apex of the root is the same as that of the cells of the second degree directed downwards which have originated in their puncta vegetationis. The oldest, outermost of them, reaches as far as the place of origin of the root, the younger, inner ones, are gradually less in proportion to their age. The oldest outermost cellular layers of the apex of the root scale off by degrees and become decayed.

The cell-multiplication of those cells of the second degree which are directed upwards tends much more to the increase of the number of cells in height than in breadth. The longitudinal division of each such newly formed cell is

* See Nägeli, 'Zeitschrift f. Botanik,' Heft 3 and 4, p. 143.

followed by division by means of septa parallel to the basal surface, and perpendicular to the longitudinal axis of the root. The outer cells of the group formed by the multiplication of those cells of the second degree which are directed upwards (those which adjoin the daughter-cells of the second degree which are directed downwards) continue to multiply for some time by division by means of septa alternately radial and parallel to the periphery. But the succession of these divisions is twice interrupted by the formation of horizontal septa in the entire mass of cells produced by the multiplication of the cell of the second degree which is directed upwards.

The adventitious roots like the adventitious buds are capable of remaining dormant for a long time. When they burst forth and become elongated, the central string of cells is transformed into a vascular bundle. The tissue immediately enclosing the latter becomes disintegrated, dries up, and ultimately disappears. Thus a hollow cylindrical air cavity is produced beneath the bark of the adventitious root. The upper surface of the root becomes covered with long papillæ which become brown in age. In very old rhizomes the cortical layer of the root usually disappears entirely; the central vascular bundles only, (whose tissue is very firm) are persistent, and have the appearance of tough, thick, deep-brown fibres.

Fruit is usually developed only on the vigorous shoots produced from the lowest internodes of a shoot of the previous year. The transition from the form of the ordinary sheathing leaves, to that of the lowest circle of sporangia is very rapid and sudden, even in those species which (like *Equisetum arvense*) have special fructifying shoots. The sheathing leaf immediately underneath the fruit is shorter and more fleshy than the others; there is no other intermediate condition. The fructification is morphologically unlimited; owing to its mode of origin its longitudinal development is not confined within bounds, any more than that of the vegetative shoots, which (at least those above ground) nevertheless do not become elongated beyond a certain extent. Each circle of sporangia makes its appearance in the form of an annular cushion underneath the

terminal bud,* like the first rudiment of the vegetative leaf, but more massive and much less elevated.

Definite points in this very flat annular wall become prominent, after the manner in which the leaf tips project above the (originally) smooth margin of the sheathing leaf. A ring of hemispherical protuberances is thus produced around the stem, which, in the growing fruit, is clearly perceptible in the third rudimentary sporangial circle, reckoning from the terminal bud downwards (Pl. XXXVI, figs. 3, 6). The normal cell-multiplication of these hemispherical cellular masses—the rudiments of the stalks of the sporangia—is similar to that of the fruit-rudiment of Pellia (Pl. XXXVI, figs. 4, 5). The development of their upper part soon exceeds that of the lower; by the pressure of their apices against one another they assume the form of hexagonal shields. On the underside, where they pass into the stalk, these shields soon exhibit at five or six points a rapid cell-multiplication produced by the division of one of the cells of the under surface of the shield. This division takes place by septa inclined in different directions, and is repeated continually in the apical cell (Pl. XXXVI, fig. 7). From five to six blunt warts of cellular tissue are thus produced on the under side of the shield: these are the first rudiments of the sporangia. Shortly after their first appearance the growth of one of the inner cells considerably surpasses that of its neighbours. The cell in question is at this time only separated from the apex of the young sporangium by a simple layer consisting of a few cells. It is the primary mother-cell of the spores; the cells surrounding it become the wall of the sporangium.

The first division of the primary mother-cell takes place by a horizontal septum (Pl. XXXVI, fig. 8). By repeated bi-partition of the primary mother-cell the number of cells destined for spore-formation is increased (Pl. XXXVI, figs. 9, 10). In the mean time the number of the cells of the wall increases much more rapidly: the latter soon consists of a double layer produced by the division of its

* The structure and mode of cell-multiplication of the terminal bud exactly correspond with that of the terminal bud of vegetative shoots.

cells by septa parallel to the outer surface (Pl. XXXVI, fig. 9). A previous division takes place by septa which cross one another in different directions, and are perpendicular to the outer surface, and by such division the circumference of the wall is increased, keeping pace with the increase in volume of the group of mother-cells. In the mean time the division by septa parallel to the outer surface occurs once more, so that now the wall of the sporagium consists of three layers of cells (Pl. XXXVI, fig. 10).

The inner one of these layers and the middle one become dissolved, and are displaced by the group of mother-cells, the size of which increases continually. The inner layer is dissolved at an early period, and the middle one shortly before the time when the mother-cells are individualised (Pl. XXXVI, fig. 13). The connexion between the mother-cells is not broken up all at once. Small groups, consisting normally of four cells, usually hang together for some time (Pl. XXXVI, figs. 11, 12). This process corresponds exactly with what takes place in the formation of the pollen of phænogams.

Each of the spore-mother-cells when free exhibits a large central nucleus, as is the case at all periods of their development, except immediately before the division of a generation of mother-cells. This nucleus, which usually has only one moderate-sized spherical nucleolus, is a globular empty cavity, having a vesicular appearance, and is filled with fluid which is less highly refractive than the thickly mucilaginous contents of the cell, which are rendered turbid by numerous fine yellowish granules. In the further progress of the development of the fruit the membrane of this nucleus is slowly dissolved: its fluid contents do not intermingle with that of the cell (Pl. XXXVI, fig. 12; Pl. XXXVII, fig. 1). In its place two large flatly ellipsoidal nuclei suddenly appear occupying almost half the mother-cell. These latter nuclei at first exhibit no nucleoli, but at a later period they contain several (Pl. XXXVI, fig. 3). In the equator of the cell, between the two nucleoli, a ring or plate of protoplasmic granules is formed near the cell-wall (Pl. XXXVII, figs. 4, 5). The outlines of the two flattened nuclei then become more

and more indistinct, and soon disappear altogether. The granules which compose the above-mentioned ring or plate, distribute themselves in the fluid contents of the mother-cell, and four smaller globular nuclei are now seen in the latter, whose appearance is as sudden as that of the two larger flattened nuclei, which took place a short time previously (Pl. XXXVII, fig. 6). They are arranged in the angles of a tetrahedron, and a septum is visible between each two of them. Introductory stages of the development of the septum may be seen in the form of thick indistinct flattened agglomerations of yellowish protoplasm. Thus the mother-cell is divided into four tetrahedral cells which are the special-mother-cells (Pl. XXXVII, figs. 7, 8).

Hitherto the development of the spores, from the separation of the mother-cell down to the minutest details, resembles that of the pollen of the Abietineæ.* This renders their further history so much the more peculiar.

The four tetrahedral cells into which the mother-cell divides, very soon become disunited, doubtless on account of the dissolution of the primary wall of the mother-cell, and of the outer layer of the walls of the four daughter-cells. They then appear in the form of perfectly spherical very thin-walled cells. A layer of granular mucilage covers the inner wall, leaving in the centre a free globular cavity filled with a thin fluid. The very flat nucleus is embedded in the protoplasmic layer. The globular cell, when lying in water, soon appears surrounded by a bright halo, formed of a layer of apparently gelatinous matter, which when treated with iodine exhibits no colour. (Pl. XXXVII, fig. 9). A very delicate membrane forms the outer boundary of this covering layer. In somewhat older sporangia this membrane appears more firm, and more distinctly separated from the inner part of the layer surrounding the globular cell, which now consists of a fluid coloured pale yellow by iodine. These stages of development of the spore-mother-cell are passed through in a very short time. In the same sporagium of *Eq. palustre* there may be found mother-cells with the primary nucleus in the act of dissolution, others with two flattened nuclei, and others with

* 'Bot. Zeit.,' 1848, p. 670.

four globular daughter-nuclei; there may also be found sets of four tetrahedral daughter-cells, individual daughter-cells, of a globular form, and lastly, others which already exhibit the transparent halo slightly developed. The appearance of the latter is not accompanied by any perceptible contraction of the contents of the globular cell. If the cells which, when treated with water, exhibit the above-mentioned halo, are examined in the fluid contents of the sporangium, their membrane appears thin and quite homogeneous even under the best microscopes. But in sporangia a little more advanced, the membrane in question under similar circumstances appears to be composed of two layers, the inner one of which is thicker and more highly refractive than the outer one. The outer layer, when treated with alcohol, contracts so as to be hardly distinguishable from the inner one. At the same time the cell-contents contract, sometimes into a globular shape, sometimes irregularly. If water is applied the outer layer swells considerably, and forms a thick, gelatinous, almost fluid covering, round the inner one, which remains unaltered. Under the further action of water this gelatinous layer is dissipated in the surrounding fluids. The effect of alcohol upon the fresh cell is to lessen considerably this power of distension. After treatment with alcohol the outer layer only swells up to a definite extent (to about three times its original size), in distilled water. If the preparation is now crushed, the swollen layer is pressed out over a wide space, and is then clearly seen to consist entirely of a homogeneous hyaline gelatinous substance, and that the granular aspect of its outer surface is owing to the attachment of small extraneous bodies. A longer exposure to the effect of alcohol often entirely destroys the capacity for distension.

Iodized solution of chloride of zinc imparts a pale blue colour to the entire mass of the outer membrane, and renders the inner one yellow. After the cells have lain in alcohol the same solution renders the outer layer pale yellow, and the inner one brown. The addition of water brings out the blue colouring in the outer layer. Ammoniated oxide of copper applied to the fresh cell causes only a slight distension of the outer layer, and hardens it so that it no

longer spreads out under pressure. Sulphuric acid dissolves the outer layer; the inner one withstands its action but assumes a brown colour. At this period of development the diameter of the cell is from 20·24 to 23·60 m. m. m. and no trace of any third inner membrane is perceptible, even when the cell is ruptured after lying in alcohol.

But when the cell has attained a diameter of from 30·3 to 37 m. m. m. a third internal covering of the cell-contents soon makes its appearance. Such a cell when placed in diluted alcohol exhibits three perfectly distinct membranes. Each of the three globular vesicles is situated excentrically in the interior of the next outer one. If the fresh cell is placed in alcohol the three membranes swell up but in different degrees: the outer one swells the most, the middle one to a less extent than the outer, and the inner one least of all. The cell-contents swell up at the same time; they always remain closely attached to the inner membrane, and cannot be brought to contract into a smaller space than the cavity of the latter. In a cell for instance whose diameter in alcohol was 30·2 m. m. m. the membrane immediately enclosing the cell contents measured (after treatment with water) 32 m. m. m.; the middle one 37·04 m. m. m., and the outer one 63·84 m. m. m.

At this stage of development the iodized solution of chloride of zinc colours all three membranes blue; the middle one changes colour first, and its colour is the most intense. If such cells, after lying in alcohol, are ruptured by pressure, the membranes, which have previously been closely attached to one another, separate; the middle one contracts to a smaller space than the outer one, and the inner one more than the middle one. After contraction they still retain the form of tense globular vesicles, and exhibit a greater thickness of wall than before. If cells fresh from the sporangium are treated with water, the outer and middle membranes often swell up to some extent: they separate from the inner layer, remaining at the same in close connexion with one another. The distended membranes are easily separable from one another by pressure, and they exhibit a scarcely perceptible increase in thickness. At this period no trace is yet visible of the course of the

spiral bands into which the outer membrane shortly afterwards divides.*

In those sporangia however in which some cells of the outer membrane exhibit traces of elater-formation and others do not, the capacity for distension of the middle membrane is far behind that of the outer one. Even in the fluid contents of the sporangium itself the outer membrane, in *Equisetum limosum*, is at a considerable distance from the middle one. Upon treatment with alcohol the middle and the inner membrane are drawn far away from the outer one whilst they remain in close contact with one another, and with the cell-contents. Upon the subsequent addition of water the inner membrane remains still in close contact at every point with the cell contents; the middle one becomes somewhat detached and often irregularly folded; and the outer layer is far removed from the middle one. With this distension of the outer membrane it becomes manifest that the latter is traversed by two left handed, parallel, spiral lines, in the course of which the membrane is thinner than in its other parts. In profile, *i. e.*, in an optical longitudinal section of the cell, I see with the best microscopes that the thicker portions of the membrane protrude *inwards* over the thinner parts (Pl. XXXVIII, fig. 10), not *outwardly*† as Sanio says ('Bot. Zeit.,' 1857, p. 661). When

* In the 'Vergleichende Untersuchungen,' p. 99, I spoke of the processes above described as consisting of the formation of a free cell (the spore) around the primary nucleus of the special mother-cell. In opposition to this, Sanio has shown ('Bot. Zeit.,' 1856, p. 181, 1857, p. 657) that *within the sporangium* the two membranes always lie close to one another, and that therefore a free cell-formation cannot be admitted. This is quite correct. Sanio further attempted to show that there could be no such thing as a centripetal spiral thickening of the outer cell-membrane, which membrane at a later period splits to form the elaters. The reasons brought forward to prove this are however not convincing. During the development of the spores of the Equisetaceæ some phenomena occur which have an important bearing upon the study of the cell-membrane, and I therefore give here in some detail the result of recent investigations of this subject. Some of Sanio's objections to my views as to the divisions of the mother-cell (l. c., 1856, p. 170) have since been abandoned by himself (l. c., 1857, p. 658). With regard to his observations on the abnormal development of certain mother-cells and the division of the primary nucleus by constriction, I will only remark that there is no analogy between such cases and the cases where the process of development is normal.

† I contend that my representation ('Vergl. Unters.,' t. xx, f. 18) is quite correct, irrespective of the fact that in this figure the thin portions of the membrane have come out disproportionately thick.

in water the outer membrane, which is in the process of being transformed into elaters, is coloured pale blue by iodized solution of chloride of zinc; in the middle layer the blue is more intense.

In sporangia a little more advanced the thin parts of the outer membrane disappear: the delicate pellicle which held together the coils of the elaters is no longer present. Fresh elaters are coloured a greyish-blue by the above-mentioned solution, with the exception of a thin outer layer which assumes a yellowish colour. By adding a quantity of water the colour of the main portion of the elaters becomes a more pure blue. After the separation of the elaters the middle spore membrane exhibits a very different reaction with iodine; it remains yellow under all circumstances, under the iodized solution of chloride of zinc, as well as under iodine and sulphuric acid. Ammoniated oxide of copper if applied to the outer membrane just after it has split to form the elaters, is very rapid in its effects. The membrane becomes distended and is gradually dissolved. Under the action of the same fluid the next inner membrane swells up into a large vesicle, without diminishing perceptibly in thickness. Its substance is then softer; by rolling it under a covering glass it is easily wrinkled. The third membrane is tightly stretched upon the cell-contents. The further action of ammoniated oxide of copper gives it a yellowish colour, but in other respects it remains unchanged.

A little later, whilst the elaters are continually increasing in breadth and thickness, the rudiment of a final innermost membrane of the spore becomes visible. If a young spore in this stage of development is detached from its elaters, and placed in alcohol, and if water be then added, the membrane next to the elaters becomes detached from the third membrane, and from the cell-contents which are closely embraced by the latter, and in which chlorophyll now begins to appear. If the spore be now ruptured by pressure, the membrane next to the elaters remains folded without changing its volume. The next inner one remains after the rupture tense as before, whilst it contracts upon a much smaller space, and now appears considerably thicker

than it previously was. It has borne a strong pressure from the expanding cell-contents, and possesses a high degree of elasticity. Its hitherto smooth outer surface now exhibits very small protuberances which give it a finely granular appearance. Its inner surface is covered by a tolerably thick layer of semi-fluid hyaline matter, which by hard pressure is partly driven out from the fissure of the ruptured membrane. If a spore in the above stage of development be taken fresh from the sporangium and treated with caustic potash, the elaters swell up; the adjoining membrane is distended into a vesicle, and usually becomes wrinkled. The third granular membrane assumes a brown colour, but in other respects remains unchanged. The fourth membrane, which is still delicate, contracts round the cell-contents, and exhibits a double outline.* The peripheral portion of the cell-contents then assumes a red colour, which never extends so far as the middle point of the cell, and which depends upon the presence of tannin.† Sometimes in spores taken from the same sporangium, like those just mentioned, the innermost layer swells up under caustic potash, and remains in contact with the granular layer. The latter may then be stripped off from the inner layer by friction with the covering glass, and will be seen to be a closed vesicle surrounding the cell-contents. Sulphuric acid immediately destroys the elaters of such spores; the next inner membrane, like the third granular layer, thereupon expands into a capacious vesicle, but resists the acid. The fourth innermost layer swells, and becomes converted into gelatine, which after the rupture of the cell is immediately dispersed in the surrounding fluid.

After the bursting of the ripe sporangia‡ the elaters, when dry, are stretched out, remaining attached to the spore by their median portion. When moistened they roll together

* Sanio, l. c., p. 665, who from its contractility, draws the conclusion that it is a primordial utricle.

† Sachs, 'Sitzungsb. Wiener. Acad.,' xxxvi, (1859) p. 21. Sanio has observed that the red colour only affects the cell-contents, l. c., p. 666.

‡ The wall of the sporangia, which consists of one layer of cells, is transformed into spiral cells. Compare Henderson, 'Trans. Linn. Soc.,' v, xviii, p. 567.

in a spiral manner, covering the spore entirely as at first. It may easily be seen by the examination of detached fragments of elaters that the rolling inwards is not accompanied by any contraction of the concave side. It follows from this that the extension of the elaters depends upon a relatively greater contraction of the *outer* layers of their tissue, a contraction which is completely balanced by moistening the elaters. By moistening the ripe dry spores the elaters are rapidly rolled inwards; almost immediately afterwards they become unrolled. Sulphuric acid and water also causes a rolling inwards of the elaters: when concentrated to a certain extent it destroys only the inner layers. The thin outermost layer, which during the formation of the inner layer was coloured yellow by iodized chloride of zinc (Pringsheim's 'Elater-cuticle,' Bot. Zeit., 1853, p. 244), remains behind in the form of a loose band. The second (now the outermost) membrane of the spore, becomes distended and detached from the middle layer by the action of sulphuric acid, whether concentrated or diluted. The inner spore-membrane is largely distended by concentrated sulphuric acid, so that it soon ruptures both the outer membranes, and emerges with the spore-contents in the form of a gelatinous globule (Pl. XXXVIII, fig. 11). The two outer membranes are not affected by heated sulphuric acid, not even by remaining in the acid for ten days. The outer layer under such circumstances remains at first as clear as glass, and afterwards only exhibits a smoky-grey colour and a granular consistency of the outer surface. The inner layer which is finely granular is coloured deep brown. After the rupture of the spore all its membranes contract considerably, so that the diameter of their inner cavity is only about half the previous size. If the rupture of the spore is effected by treatment with sulphuric acid the contraction of the middle (third) membrane, and consequently the elasticity upon which this contraction rests, appears to be altogether unaffected, and that of the outer membrane is but slightly acted on. After the bursting, by pressure, of the fresh, ripe, detached spore, the outer boundary only of the innermost (fourth) membrane is sharply defined; the inner side of the latter mem-

brane becomes by degrees a half solid gelatinous layer. It is not until germination that this membrane becomes smooth and firm on both sides. The expansion of the cell-contents and of the innermost membrane which takes place when the spore is sown upon moist ground, very soon ruptures the outermost of the three membranes, and shortly afterwards the middle one also, and both are stripped off. The substance which is coloured red by caustic potash remains attached to the inner wall of the innermost membrane after the latter has become free, and even for some time after its division into two cells. This substance has the form of a layer composed of very minute particles, and it may be detached by pressure from the cell-membrane.

Two facts in the process of development of the spores of the Equisetaceæ are of general interest. The spore-membrane is here seen to increase in thickness after two different modes of growth occurring side by side. There is growth by apposition and growth by intussusception. To the former is to be attributed the origin of the third and fourth membranes, which are evidently produced from the gradual hardening of layers of gelatinous matter spread over the inner surface of the previously existing membranes. To the latter belongs the centripetal growth of the elaters, after their separation from one another, and the centrifugal growth of the second and third membrane during and after the formation of the fourth; a growth which exhibits itself in the granulation of the outer surfaces of both these membranes. The second point, however, is the more important one, viz., the remarkable modifications of the physical properties and chemical reactions which each of the four membranes of the spore undergoes during the process of development. Each of them exhibits during a certain period of its existence the assumed characteristic relation between cellulose and iodine and sulphuric acid; but this relation is never seen in the earliest states of development, nor is it constant. The outer layer of the first membrane (*i. e.*, the elaters), and of the fourth membrane (even after the commencement of germination), assume in the course of development the character of a cuticle; the second and third maintain that

character throughout. The three outer membranes when young are far more capable of distension than at a later period, and during this condition the second and third membranes are not without a high degree of elasticity, which diminishes as the capacity of distension becomes less, or even disappears altogether.

Sanio* has made some interesting observations upon the abnormal formation of elaters out of the membranes of mother-cells in which the division into four daughter-cells has been suppressed. Since these observations it can hardly be doubted that the outermost membrane, which is transformed into elaters, must be looked upon as their special-mother-cell. The Equisetaceæ, therefore, exhibit the rare circumstance of the persistence of the membrane of the special-mother-cell, a fact which, as far as I know, occurs in phænogams only in *Maranta Zebrina*. During the transformation of the membrane of the special-mother-cell into elaters a change in the substance of the membrane appears to take place. Spiral strips of the membrane become thinner and ultimately disappear, whilst other strips parallel to these increase in thickness. The differentiation of the membrane in a superficial direction into strips of different characters, may be compared with its differentiation in the direction of the thickness into two layers of different properties.

In the ripe spores the central globular nucleus is very clearly visible floating in the yellowish oleaginous fluid contents, in which, even before the shedding of the spores, numerous chlorophyll granules are seen. The number of the latter increases rapidly when the spores are sown on moist ground. After a few hours the primary nucleus vanishes. In its place two new ones make their appearance, the position of which can often only be made out by means of the agglomeration of chlorophyll-granules in their neighbourhood (Pl. XXXVIII, fig. 12). Between the two a septum is formed, dividing the spore into two very unequal parts (Pl. XXXVII, fig. 13). One of these, the larger one, contains almost all the chlorophyll-granules of the cell: the other has hardly anything but finely-granular

* 'Bot. Zeit.,' 1857, p. 667.

mucilage. This latter cell usually constitutes the first radicular hair of the growing prothallium (Pl. XXXVII; figs. 14—16).

In *Equisetum limosum* and *palustre* the upper chlorophyll-bearing cell divides immediately by a vertical or strongly inclined septum (Pl. XXXVIII, figs. 15, 16). In *Equisetum arvense* the cell often expands to a very considerable extent before it divides, especially when the spore is sown in a very moist shady place (Pl. XXXVIII, fig. 19). The formative matter—protoplasm mixed with numerous chlorophyll-granules—is accumulated at the apex of the upper cell, which is turned away from the rooting end of the growing prothallium. This mucilaginous mass usually, but not always, surrounds the nucleus. The latter dissolves gradually and two new ones take its place (Pl. XXXVIII, fig. 19). A transverse septum, which makes its appearance between the two, divides the large chlorophyll-bearing cell into an upper, smaller cell, destined for further active division, and a lower, distended, permanent cell (Pl. XXXVII, fig. 20). The basal cell often grows into a tubular root after the previous growth of one or more capillary roots from the free outer wall of the younger cells. Frequently, however, this does not take place (Pl. XXXVII, fig. 20).

The further development of the prothallium is very various. There is hardly any organ of the higher plants in which there is so little regularity of cell-multiplication. Usually there is a tendency to longitudinal growth by the repeated division of one or more apical cells by means of transverse septa, and also to the division of the cells of the second degree by longitudinal septa. Lateral shoots are very often formed. They are produced by the protrusion of the wall of a somewhat older cell, and the subsequent separation of the protuberance from the primary cell-cavity by means of a transverse septum (Pl. XXXVII, fig. 20). These adventitious shoots exhibit the like forms of cell-multiplication as the primary shoots, which they often surpass in vigour (Pl. XXXVII, fig. 22). In other cases there is a manifest bifurcation of the fore-end of the prothallium produced by the parting asunder and development of two apical cells (Pl. XXXVII, figs. 17, 21). When the cells

of the prothallium have reached the stage at which the protoplasm of their contents clothes the inner wall in the form of a thin layer, they have a manifestly vesicular appearance. I have often clearly observed their multiplication by division (Pl. XXXVII, fig. 20). Mucilaginous threads radiate from the nucleus.

However various the ramifications of the prothallium may be at first, the final result is always the same. One or more (five at the most) of the numerous shoots develope themselves much more vigorously than the others in length, breadth, and thickness. Their outline resembles to some extent that of the prothallia of the ferns. The subsequently formed capillary roots of the prothallium are produced almost exclusively from their under side. Sexual organs are mainly produced from these principal lobes; they seldom occur on other parts of the prothallium.

The prothallia of *Equisetum arvense*, *pratense*, and *palustre*, are distinctly diœcious. The individuals which bear antheridia produce them very plentifully, but yield archegonia only in the rarest instances, and then upon late shoots of the base of the prothallium. These may be considered as new individuals, by analogy to the processes which spring from the marginal cells of old fern-prothallia. The male prothallia do not attain the full size of the females. They consist normally of only one or two thickly fleshy expansions of cellular tissue, whose margins bear the antheridia, and also some thin membraneous barren shoots. Their chlorophyll contrasts with that of the female prothallia by a manifest tendency to a yellow colour. The deep-brown colour which is assumed by empty antheridia, imparts a diseased appearance to the male prothallia at an early period.

The production of an antheridium is preceded by frequently repeated division of one of the marginal cells by means of septa inclined alternately in two directions (Pl. XXXVIII, fig. 24). The cells of the second degree divide by radial longitudinal septa, and each of the three-sided cells thus formed divide into inner and outer cells by septa parallel to the axis of the organ. The latter become the covering layer of the antheridium, and numerous chloro-

phyll vesicles are spread over their inner wall. The median cavity of the cell is filled with a watery fluid. The axile cells of the young antheridium form an oval group, composed of four longitudinal rows of cells, and contain finely-granular mucilage (Pl. XXXVII, fig. 24). By rapidly repeated division in all three directions of space they are transformed into a mass of small tessellated cells, which at first are in very close connexion with one another. In each of them a flattened ellipsoidal cellule is formed (Pl. XXXVII, fig. 25), in the interior of which a small vesicle with less highly refractive fluid contents is sometimes visible (Pl. XXXVII, fig. 26). The walls of the firmly adherent cubical cells are now dissolved, and the ellipsoidal cellules become free. A gelatinous mass, spread over their inner wall, soon begins to be visible; it forms an imperfect ring parallel to the major axis of the ellipsoidal cell. This is the first indication of the nascent spermatozoa (Pl. XXXVII, fig. 27). Numerous mucilaginous granules remain for a long period in the middle point of the cellule, even until the ripening of the antheridium.

The apical cells of the covering layer of the antheridium, which are usually eight in number, contain little or no chlorophyll. In the elongated antheridia of *Eq. limosum* the cells adjoining these apical cells have also very little chlorophyll (Pl. XXXVII, fig. 24). When the organ is ripe the apical cells part asunder, and the cellules enclosing the spermatozoa ooze slowly out.

These cellules are larger in Equisetum than in any other known plant. In *Eq. arvense* their diameter attains $\frac{1}{150}'''$. When the vesicle is ripe the spermatozoon soon becomes partly free, apparently by the distension and dissolution of parts of the wall of the enveloping cell. The numerous cilia on its thick fore-end commence their active oscillating motion, by means of which the spermatozoon with the attached vesicle moves rapidly about in the water on the slide. The spermatozoon seldom becomes entirely free from its mother-cell. When it does so, it has the form of a spiral vermiform body, consisting of a mucilagino-gelatinous substance becoming dark-brown under iodine. Its fore-end, which is the thicker of the two and slightly compressed laterally,

forms two narrow closely approximated turns of a (usually) left-handed spiral. These turns alone bear the cilia. During the rapid motion of the spermatozoon in water its wider, final turn, upon which the cilia are wanting, appears to be somewhat reduced in size (Pl. XXXVIII, fig. 28), but when the spermatozoon is killed with iodine, it appears on the contrary considerably enlarged (Pl. XXXVIII, figs. 30—33). This remarkable phenomenon depends upon an organization hitherto (as far as is known) unique in the vegetable kingdom. The end of the spermatozoon bears on the inner side of its ultimate turn a wide fin-like process, consisting of a delicate membrane, which during the motion of the spermatozoon glistens like the undulating membranes of the spermatozoa of toads and Tritons. When the motion becomes more active the membranous margin becomes invisible like the cilia; it is only clearly visible when the vital activity of the spermatozoon is on the decline (Pl. XXXVII, figs. 30—33). The undulations of the fin last longer than the oscillations of the cilia. The hinder end of the spermatozoon appears still somewhat pointed when the quiescent cilia of the fore-end are already visible. The hinder end of the spermatozoon is of a very delicate half-fluid consistence; it attaches itself easily to any object, and is then drawn out into long threads. It often happens that a spermatozoon drags after it the empty membrane of the mother-cell attached to one of such threads, or that it fastens itself to a capillary root of a prothallium (Pl. XXXVIII, fig. 28^{b}). Spermatozoa whose motion, after many hours continuance, ends spontaneously, always exhibit a thin caudal appendage often of very considerable length. The substance of their hinder end has doubtless been drawn out into such threads, in consequence of the spermatozoon having attached itself to some body during its motion, and then torn itself away. The substance of such spermatozoa exhibits, by the presence in it of vacuoles, manifest traces of a state of distension.* If the spermatozoa are killed with iodine they

* In the 'Veigleich. Unters.,' p. 101, I treated the whip-shaped elongated form of the hinder end as a peculiarity common to the spermatozoa of Equisetum, an assumption which was grounded upon the frequent occurrence of such peculiarity.

usually unrol themselves like a snail (Pl. XXXVII, figs. 31—33); it is but rarely that the individual turns remain at a distance from one another, as is the case during the motion. The motile cilia appear stiff and extended when the spermatozoon is quiescent; their direction is not radial to the axis of the spiral of the spermatozoon, but is turned backwards.

The mode in which portions of the spermatozoon remain attached to the mother-vesicle is very various. Very frequently the thick fore-end remains inside the spherical vesicle, the lower turns protruding out of the fissure, and causing by the oscillation of their cilia a restless reeling motion of the organ and its mother-cell. More rarely the fore-end is free and the hinder-end enclosed in the vesicle. In such cases the motion is more regular and more rapid. It more often happens that the cilia of the thickest end of the spermatozoon protrude out of a fissure in the vesicle. The continual rolling motion of such spermatozoa very much resembles that of many infusoria.

I have seen the motion of the spermatozoa of *Equisetum arvense* last for five hours. The sensitiveness of the spermatozoa to external influences appeared to me much less than that of ferns. Water containing much gypsum, which acted in a decidedly injurious manner upon the spermatozoa of *Asplenium septentrionale*, had not the slightest effect upon those of *Eq. arvense, palustre,* and *limosum*.

In *Eq. limosum* I found the first ripe antheridia five weeks after the sowing of the spores (on the 1st of July), in *Eq. arvense* thirteen weeks after (at the end of July); in one case four weeks only after the sowing (at the end of May). The number of the antheridia upon one prothallium is sometimes as many as sixteen in *Eq. arvense*. The inner wall of the cavity of antheridia which have discharged their contents assumes a deep brown colour. The escape of the cells enclosing the spermatozoa certainly takes place spontaneously; heaps of agglomerated dried mother-cells of spermatozoa are often found at the apex of empty antheridia.

Numerous obstacles seem to interfere with the natural germination of the Equisetaceæ. Although I have often searched

for them, I have never found the prothallia of any species in their natural state. Even under culture, the greater number of the prothallia decay before the development of antheridia, or are destroyed by insects, or by an overgrowth of Vaucheriæ, Oscillatorieæ, or proembryos of mosses. Before 1852 very few of the prothallia of *Equisetum arvense* which I had cultivated lived beyond the fifth month after the sowing. They were all of the male sex. In some I observed the formation of a short, flat, lateral shoot, which produced the rudiments of archegonia. This was the only instance of departure from the diœcious character which ever occurred to me in the prothallia of Equiseta.

Those prothallia of *Eq. arvense, variegatum,* and *palustre,* which produce archegonia never produce antheridia.* They ramify to a much greater extent and become far more vigorous than the male prothallia. A female prothallium is normally a circular combination of from three to six fleshy masses of cellular tissue, which bear very numerous green crisp shoots of more delicate texture, and from a quarter to half an inch in diameter. The form very much resembles that of young plants of *Anthoceros punctatus.*

When male and female prothallia are produced from spores sown contemporaneously, the archegonia of the female prothallia appear much later than the antheridia of the male ones; the younger female prothallium would seem to be sterile. The spores from which female and male prothallia originate are exactly of the same size and quality. External circumstances seem to have an influence upon the germinating prothallia. A dry place exposed to light seems decidedly to favour the development of male prothallia of *Equisetum arvense.* The spores of *Equisetum arvense* and *pratense* when sown artificially produced principally male prothallia,† and those of *Equisetum palustre*

* On the other hand Bischoff has found the prothallium of *Eq. sylvatium* bearing archegonia on its older portions and antheridia on its younger shoots. ('Bot. Zeit.,' 1853).

† In 1849, 50, and 51, I obtained only male prothallia, upon which rudiments of archegonia appeared only at a late period, and then only upon adventitious shoots. In the summer of 1852 the number of male prothallia was greater by about one half than that of the female ones. That summer seems to have been especially favorable to the germination of Equisetum. Cultivated specimens of *Equisetum variegatum* shed spores at the beginning of May. About the middle of July female prothallia, which were present in great numbers, developed small leafy plants.

(according to repeated experiments) only female prothallia.

The archegonia are produced by the multiplication of individual cells of the fore-edge of the thick, fleshy lobes of the prothallium. After the commencement of the formation of the archegonium the mass of cellular tissue to which the organ is attached usually continues to grow underneath it, so that the archegonia, like those of Pellia, are afterwards situated on the surface of the prothallium. A small, thin, membranous shoot of the prothallium is usually formed near each archegonium (Pl. XL, fig. 1).

The mother-cell of an archegonium which, like its neighbours, contains chlorophyll, only differs from the latter by its greater abundance of protoplasm. After its free upper wall has become considerably curved, its first division takes place by a horizontal membrane. The lower of the two halves, which is entirely sunk into the tissue of the prothallium, becomes the central cell of the archegonium, the aperture of the latter being formed by repeated bi-partitions of the upper half.

The first of these partitions takes place by a vertical longitudinal septum. Another septum, also vertical and at right angles to that just formed, appears immediately in each of the two newly formed cells. The four cells surrounding the central cell, which in the mean time has become remarkably curved above, grow uniformly upwards, and are at the same time divided by horizontal transverse septa—exactly in the same manner as the four vertical-cells of the fruit rudiment of a Jungermannia.* Thus a cylinder is formed projecting above the central cell of the archegonium, composed of four longitudinal rows of cells (Pl. XXXVII, figs. 35—37). The upper pair of cells undergoes considerable elongation, which afterwards takes place also in the next adjoining pair, though in a less considerable degree. The two lower pairs of cells of the neck of the archegonium become elongated upwards, but hardly perceptibly so; however, the incipient multiplication of the cells adjoining the central cell extends to the two lower pairs of cells, or at least to the lowest of them, the division taking place by means of septa alternately perpendicular

* 'Vergl. Unters.,' pp. 18, 38.

and parallel to the walls of the central cell. In consequence of these divisions the central cell of the archegonium, when fully developed, appears to be surrounded by one or two epithelioid layers of cells (Pl. XXXVIII, figs. 1—4).

Inside the central cell, during the first stage of development of the archegonium, there is formed a daughter-cell, —the *germinal vesicle*. It originates round a secondary nucleus, which makes its appearance in the apical arch of the cell (Pl. XXXVII, figs. 35, 36), sometimes as early as the commencement of the formation of the transverse septa of the two pairs of cells which form the neck of the archegonium (Pl. XXXVII, fig. 35). It grows gradually, and during the formation of the archegonium displaces more and more the contents of the central cell, especially the second nucleus of the latter, which exists during its formation (Pl. XXXVIII, fig. 1). When the archegonium opens, some granular mucilage, the last remnants of so much of the contents of the central cell as has not been absorbed in the formation of the germinal vesicle, seems to be usually spread over the outer wall of the free spherical cell (Pl. XXXVIII, fig. 2).

The four longitudinal rows of cells which form the neck of the archegonium now become disconnected at their edges. An open canal is formed leading to the central cell and traversing the longitudinal axis of the cylindrical neck. This canal is the entrance to the archegonium. The four elongated cells of its mouth bend semicircularly backwards by which means the archegonium assumes a very strange appearance; it resembles an anchor with four flukes or arms (Pl. XXXVIII, figs. 2, 3, 4, 6). The arched cells of the mouth when they part asunder contain no solid matter; the few chlorophyll vesicles as well as the nucleus of the cell have disappeared. The same is the case with the four cells which support those last mentioned. The free neck of the archegonium is transparent like glass.

There is far less difference between the structure of the archegonia of the Equisetaceæ and those of ferns than there is between the antheridia of the same plants. The former agree in all essential features with those archegonia of the Polypodiaceæ in which the neck consists only of four longi-

tudinal rows of cells. It may be asserted that the Equisetaceæ on account of the diœcious nature of their prothallia, and the constant similarity of the structure of their archegonia with that of the archegonia of the Rhizocarpeæ, especially of Pilularia, form the transition from ferns to the Rhizocarpeæ.

Male and female prothallia grow in the closest proximity, their shoots often intermingling with one another. The access to the archegonia, which is afforded to the spermatozoa not only by every rain but also by every heavy dew, is rendered still easier by the force with which, on the spontaneous opening of over ripe antheridia,* the spermatozoa still enclosed in their mother-cells—are ejected. I found in the canal of a recently impregnated archegonium mucilaginous masses closely resembling defunct spermatozoa (Pl. XXXVIII, fig. 4).

The first visible change in an impregnated archegonium is the closing of the lower end of the canal, caused by the horizontal expansion of the cells of its walls (Pl. XXXIX, fig. 4, Pl. XL, figs. 1—3). This closing is accompanied by the further multiplication of the cells of the tissue surrounding the central cell. These cells divide repeatedly by longitudinal and transverse septa; the division is particularly active in the cells of the epithelium-like layer which adjoins the central cell. The impregnated germinal vesicle has in the mean time become somewhat larger. Its nucleus has disappeared, and a layer of finely granular protoplasm lines its inner wall (Pl. XXXVIII, fig. 4). Now for the first time—after the obliteration of the lower end of the canal—the series of divisions commences by which the embryo is produced.

The germinal vesicle is first divided by a septum inclined to the longitudinal axis of the archegonium. The two halves are again immediately divided by transverse septa at right angles to those just formed. Sometimes the upper and sometimes the lower of the two first cells of the rudimentary embryo takes the lead in this division (Pl. XXXVIII, figs. 5, 6).

* It is at this time only that the small delicate crown represented by Thuret ('Ann. d. Sc. nat.,' iii S., vol. xvi, pl. 16, f. 1) is formed.

At this time or a little later the recurved cells of the aperture of the archegonium shrivel and fall off. The four elongated cells of the neck of the archegonium upon which they are borne also lose their vitality. Their walls, so far as they form the canal of the archegonium, assume a dark brown colour.

The number of the archegonia of a vigorously developed prothallium varies from twenty to thirty; it exceeds therefore that of the antheridia of even the largest male prothallia. Usually more than one archegonium is impregnated. I counted as many as seven embryos in one and the same prothallium. The brown colour of the unimpregnated archegonia extends not only over the walls of the whole canal—which remains open—but also over the central cell and its contents (Pl. XXXVIII, fig. 3).

The first axis of the embryo (which remains undeveloped) has its origin in a series of repeated divisions of the terminal cell commencing in the three-sided cell which includes the lower end of the embryo rudiment (Pl. XXXVIII, figs. 7—10; Pl. XL, figs. 1—3). The cells of the second degree divide at first only by longitudinal and transverse septa perpendicular to the free outer surfaces (Pl. XXXVIII, figs. 7, 8; Pl. XXXIX, fig. 1); at a later period septa, parallel to these surfaces make their appearance and form inner cells. A similar cell-multiplication commences in the one lateral cell of the 4-cellular-embryo-rudiment. The lines in which the first septa of the lateral cell intersect are parallel to the longitudinal axis of the archegonium (Pl. XXXVIII, figs. 7—10). A side shoot of the embryo is thereby formed—the second axis of the germ plant, its first leaf-bearing shoot. By the considerable growth in thickness of the primary axis below the place of origin of the secondary one, and still more by the upward curvature of the latter during its development, the rudiment of the secondary shoot is soon brought almost to the apex of the globular cellular mass which now constitutes the embryo—to within a small distance from the locus of the lower end of the canal of the archegonium which is now entirely obliterated (Pl. XXXIX, figs. 4, 5).

Up to this stage the rudiment of the embryo may be

detached without much difficulty. From this time however the cells of the surface of its primary axis become more and more closely connected with the neighbouring cells of the prothallium, whilst the latter—in some of which multiplication is continually going on—are more and more compressed and at last entirely absorbed by the rapid increase in size of the new plant.

The end of the secondary axis of the embryo resembles at an early period both in its form and in the mode of multiplication of its cells the terminal bud of a shoot of a developed Equisetum. The comparatively large apical cell and the ladder-like arrangement of the cells of the second degree are clearly distinguishable in the sharply conical wart of cellular tissue (Pl. XXXIX, fig. 4). As soon as the bud has assumed this form, it produces its first leaf, which like those of the developed plant is a closed, annular sheath of uniform height (*a*, fig. 4, Pl. XXXIX). The margin of this sheath is elongated upwards by contemporaneous division of its cells by means of septa inclined alternately inwards and outwards, and after some time it forms *three* lobes, which at first are blunt, but soon become pointed (Pl. XXXIX, fig. 5).

Contemporaneously with these three pointed processes of the first sheathing leaf the first adventitious root of the germ plant becomes visible. Originating in the multiplication of a cell of the inner tissue of the primary axis, it appears at first in the shape of a small, semicircular knob on that side of the embryo which is turned away from the secondary leafy shoot (Pl. XXXIX, fig. 5). The root grows in length by the multiplication of a cell of the interior of its apex like the root of the developed plant, and penetrates vertically downwards into the tissue of the prothallium (Pl. XL, figs. 2, 3). At last it breaks through the latter and makes its way for some depth into the soil. A short time afterwards the upward growing leafy shoot is sent forth from the prothallium. It consists of a small number, from ten to fifteen, of elongated internodes. All its sheathing leaves have three teeth, a rule which applies to *Equisetum arvense*, *E. pratense*, and *E. variegatum*.

After the prothallium has sent forth the root and the

leafy shoot, vascular bundles are formed in the interior of the two organs: in the stem there are three arranged in a narrow circle; in the root one single axile bundle. In the first node of the germ-plant, at the place where the first leafy branch and the first adventitious root branch off from the primary axis, all the cells into which the vascular bundles of both unite, are transformed into short annular and spiral cells, forming a closed ligneous mass without pith (Pl. XXXIX, fig. 6). The primary axis of the embryo, which is far less developed in the Equisetaceæ than in the ferns and Rhizocarpeæ, and which now stands at the side of the germ-plant, remains devoid of vessels. Its cells, which now contain much chlorophyll, become elongated upwards.

When the first leafy branch has reached a certain stage of development, an adventitious bud is produced in the interior of its cortical tissue by the multiplication of a cambial cell of its base, at the elevation of the solid ligneous mass of the first node. This bud is situated on that side of the leafy shoot which is turned away from the primary axis of the germ plant and below the depression formed by the two lobes of the first sheath (Pl. XXXIX, fig. 6). In its position as well as in its mode of development it corresponds entirely with the adventitious buds, by which all the ramification of the developed Equisetum is effected. It grows rapidly and vigorously and breaks through the bark of its mother-shoot into the open air. It is distinguished from the first leafy axis by having sheathing leaves with four teeth, and at first also by its pale yellow, ivory-like colour. The new shoot, which is far more vigorously developed than the first shoot, is the second link in the series of shoots originating from the adventitious buds of the lowest sheaths. It is by means of these latter shoots that the vigorous shoots with many-toothed sheaths and more ample ramifications are produced from the delicate primary stem which bears leaves with three teeth. The basal adventitious buds of the above vigorous shoots at last become fruit-bearing stems.

Sometimes the third, and if not the third, one or more of the subsequent principal adventitious buds (by which the duration of the germ-plant is secured) assume in the

course of their development a lateral, or downward direction, passing into the soil, and thus forming the first horizontal subterranean rhizome of the Equisetum. The sheathing leaves of this subterranean axis—which produces a large quantity of adventitious roots—have also four teeth. The shoots however which proceed from the bases of their sheaths, of which some grow up to the light, and others pierce vertically downwards to a great depth in the soil, are considerably more vigorous than all the previous ones and bear sheaths with five teeth.

Adventitious buds are produced at the bases of the upper sheathing leaves of the first shoots of the germ plant. In *Equisetum arvense* one or two only and these rarely and irregularly break through the bark of the mother-shoot, and when developed form leafy branches of very limited longitudinal growth. The limited number of whorls (amounting on the first axis to barely three, and on the succeeding axes to not more than four), forms a striking contrast with the rich ramification of the vegetative shoots of old individuals. The formation of dwarf shoots occurs only rarely and exceptionally on those branches.

The development of the germ-plant under favorable circumstances is very rapid and vigorous. Germ-plants of *Equisetum arvense*, produced from the prothallium in the first week in June, formed by the beginning of August seven generations of shoots, the last of them being then a foot high, and $1\frac{1}{2}'''$ in diameter, though bearing only four-toothed sheaths. The strong side-shoots of subterranean rhizomes became visible about the end of August.

The reproduction of the Equisetaceæ from spores long remained a mystery. Vaucher* in the spring of 1822 first brought forward the results of experimental sowing of the spores, and he was followed by J. G. Agardh.† They both saw only the first stages of development of the prothallia, which Agardh described as cotyledons on account of their two-lobed form. In the following year Vaucher published some observations which gave a full

* 'Mem. Soc. de Genève,' i, (1817) p. 329.
† 'Mem. du Museé d'Histoire Nat.,' vol. ix.

account of the external phenomena of the germination. Vaucher found* that spores of *Eq. Telmateia* and *palustre*, when sown in flower-pots, became swollen, and divided at the apex first into two, and then into several lobes. These lobes sent forth rootlets which affixed themselves to the ground, and ultimately formed bright green patches sometimes as much as a line in diameter, and resembling a small Aneura. They remained in this condition for about two months without growing perceptibly. At last a green point grew out from the middle of the patch, which point, as it became larger, exhibited a frill at its base, then a second, and then a third frill, from the apex of which the young stem arose. Vaucher distinguished the two kinds of roots of the prothallium and of the embryo; he stated that the first formed roots were numerous, although thin and stunted; but that a vigorous root was produced from the stem of the young Equisetum, and penetrated perpendicularly into the ground.

Vaucher's observations remained for some time quite unsupported. In 1826 Bischoff's experiments only resulted in the production of prothallia, all of which afterwards decayed. He showed, however, clearly,† that the processes described by Agardh and Vaucher as cotyledons, were only an imperfect, or intermediate germ-growth (a proembryo or prothallium), which, as in most other cryptogamic plants, afterwards became transformed into a true embryo. In the autumn of the same year Bischoff supplemented his observations by publishing the result of his examination of some germ-plants of *Eq. palustre*, found in the autumn of 1827, in their native habitats.‡ He observed that the young germ-plants burst forth from the interior of the prothallium, and he disproved Vaucher's statement,—viz., that the root which penetrates into the earth is afterwards transformed into the rhizome—by showing that at a very early period the germ-plant produces lateral shoots, whose growth from the commencement follows a horizontal or downward direction. He noticed also

* 'Mem. d. Musée.,' vol. x, 1823, p. 429.
† 'Kryptog. Gewächse,' i. Nurnberg, 1828, p. 43.
‡ See 'N. A. A. C. L.,' vol. xiv, p. 785.

the development of more than one germ-plant out of the same prothallium. At that time he quite overlooked the sexual organs. Thuret ('Ann. d. Sc.,' iii ser., 1849, vol. v, p. 5,) gives the first account of the antheridia of Equisetum, and the discovery of the archegonia seems to be due to Bischoff. Mettenius mentions ('Beiträge zur Bot.' Heidelberg, 1850, p. 22), that archegonia resembling the defunct archegonia of ferns were found upon a small piece of a prothallium which he saw in Bischoff's possession. Milde in 1850 ('Linnæa,' xxiii, p. 545), gave a more complete account of the structure of the antherida and spermatozoa. A little later I myself explained the development of the antheridia and spermatozoa, and figured the first stages of development of the archegonia ('Vergl. Unters.' Leipz., 1851, p. 102, Pl. xx, fig. 62). Soon afterwards, Milde also observed the neck of the archegonium, but without knowing what it was ('N. A. A. C. L.,' xxiii, 641). In 1852 I observed the development of the embryo ('Flora,' 1852, p. 385), and almost at the same time Milde discovered archegonia, and he published his observations soon after mine ('Flora,' 1852, p. 497). I made some further remarks upon my previous observations in the fourth volume of the 'Transactions of the Royal Society of Saxony,' p. 168.

CHAPTER IX.

OPHIOGLOSSEÆ.

The germination and development of Botrychium Lunaria Sw.

The Moonwort germinates underground. Germ-plants* are sometimes found in the neighbourhood of full-grown individuals in places where the plant is common. They are not unlike torn fragments of branched roots of the plant itself (Pl. XLII, figs. 2—5), but upon careful examination they are found to be organically closed at all ends. At the point of junction of the roots, a prominent knob is found (Pl. XLII, figs. 4, 5). A microscopical analysis of the latter leads to the discovery of a bud buried in a deep, almost closed depression. In September, 1854, Irmisch and I discovered at a depth of from one to three inches under the surface of the earth, not only a series of productions undoubtedly transitional between germ-plants and full-grown Botrychia, but also germ-plants, to which the prothallium was still attached. The prothallium of Botrychium (Pl. XLI, fig. 5), is an oval mass of firm cellular tissue, whose larger diameter does not exceed half a line, and is often less. It is light brown on the outside, yellowish-white on the inside, and furnished on all sides with scattered, rather long, capillary roots. The cells, whose size diminishes from the middle of the prothallium towards the periphery, are filled with large and small lumps

* The germ-plants upon which these observations were made came from the neighbourhood of Sondershausen. I am indebted to my friend Professor Irmisch for them.

of a semi-transparent substance, which is not rendered blue by iodine. On the side turned towards the surface of the earth the prothallium mostly produces antheridia, and on the opposite side archegonia. The former have the appearance of cavities in the mass of the prothallium, which open outwards with a very narrow mouth (Pl. XLI, figs. 5, 6, 10^b.) The spermatozoa are hardly distinguishable from those of the Polypodiaceæ, except in being half as large again as the latter. The walls of empty antheridia are coloured light brown, and are covered with a granular substance. The archegonia (Pl. XLI, figs. 5, 10^b), are entirely buried in the prothallium, but agree in other respects with those of the ferns. Spores sown artificially swelled to twice their natural size, but underwent no further change. The membrane of a spore thus swollen was found attached to a prothallium, and was recognisable by the three prominent ridges of the outer surface, which meet at angles of 120° (Pl. XLI, fig. 7).

The position of the embryo with regard to the prothallium differs widely from what occurs in the Polypodiaceæ and Rhizocarpeæ. Botrychium in this respect is allied to those vascular cryptogams, whose prothallium, like that of the Ophioglosseæ, is devoid of chlorophyll (Isoetes, Selaginella). The punctum vegetationis of the embryo lies near the apex of the central cell of the archegonium. The first roots originate underneath it near the base of the archegonium (Pl. XLI, fig. 6^b; Pl. XLII, fig. 1^b). In consequence of the downward direction of the mouth of the archegonia, the embryo has to turn half round in order to give its bud an upward direction, so that the prothallium is found attached to it laterally. The youngest germplants found attached to prothallia, exhibited at least two roots, and also near the punctum vegetationis, a more or less developed hemispherical or oval knob (Pl. XLI, figs. 8—10). The outside of the latter (on account of the colour) bears only a distant resemblance to the roots: its internal structure differs widely from theirs: the hemispherical body consists of wide parenchymatal cells, which become gradually smaller and flatter towards the outer surface: a rudimentary vascular bundle consisting, with

the exception of vessels, only of thin-walled prosenchymatal cells, extends from the nearest vascular bundle of the root for a short distance into the mass of cellular tissue. This structure, and also the position of the knob on the germ-plant, correspond exactly with the structure and position of the organ found on the embryo of the Polypodiaceæ and of other vascular cryptogams, which I have treated as the continuously developing primary axis of the embryo—with the primordial tissue of the embryo, which bears on its lateral surface the formative cells for further development.*

In Botrychium this primary axis, if unusually developed in thickness, may protrude laterally out of a fissure of the prothallium. The roots originate above the knob, the oldest and longest of them being the nearest to it. The direction of the roots is usually opposite to that of the knob. The punctum vegetationis—the growing end of the secondary axis of the embryo—occupies the highest point of the germ-plant (Pl. XLI, fig. 10^b; Pl. XLII, fig. 1^b). This bud, which consists of a flatly-conical group of thin-walled cells, is situated at the base of a narrow, short, transverse fissure in the blunt apex of the germ-plant, *i. e.*, the narrow opening of the vaginated scale-like first frond of the latter (Pl. XLII, fig. 1^b). Germ-plants less developed than those above described were also found in quantities (Pl. XLII, figs. 2, 3). They consisted only of the globular knob, and the first or the first and an incipient second root. The punctum vegetationis lay immediately on the upper surface of the knob. In these plants no trace of the prothallium could be perceived. They were probably of the same age as those above mentioned, but stunted and arrested in their development.

The nature of the punctum vegetationis of the germ-plant of Botrychium is a matter of special interest, inasmuch as it must afford material assistance in deciding which of two opposite opinions is the correct one. Röper† assumed that the true stem rises vertically, but owing to the non-development of the internodes, imperceptibly; that it produces two leaves or fronds every year, whose stalks grow together

* 'Griesebach Jahresber.,' 1852, p. 404.

† 'Linnæa,' vol. i, p. 460; 'Flora Mecklenbergs,' vol. i, p. 110.

upwards for some distance, and consequently enclose the true apex of the stem, together with the bud which consists of two leaves corresponding with the former in every respect. Presl ('Tent. pterid,' suppl., p. 41) has modified this view. He considers the fertile and the sterile frond as only segments of one and the same leaf, the under segment of which becomes fruitful, whilst the upper remains leaf-like. Mettenius ('Farrne des botan. Gartens zu Leipzig,' 1856, p. 119) and Röper also quite lately ('Bot. Zeit.,' 1859, p. 244) have arrived at the same opinion. Braun,* on the other hand, asserts that "the cellular body from which in Ophioglossum the leaves are produced cannot be a special sheathing leaf, nor even of the nature of a stipule or ligule, but it is a cellular body which surrounds the centre of growth, and inside which the leaves are formed in successive spirals, and there remain. Within this body each leaf forms its own cell, which enlarges with the growth of the leaf, and becomes gradually elevated in a conical form, and ultimately pierced in a sheath-like manner. The fructification of Ophioglossum is axillary; it is the only leaf which comes to perfection from a bud in the axil of a sterile leaf. . . . . Botrychium does not possess the enveloping cellular body, but on the other hand, in this genus, the leaves form their own sheaths." I have myself attempted to show that the most striking feature suggested by Braun exists also in Botrychium, for I assumed that each of the contemporaneously developed pairs of fronds originated in an entirely closed cavity, being the base of the next older pair of fronds. According to this the stem of Botrychium would be a sympodium of the basal portions of successive yearly shoots.† Schacht also agreed in this view when he asserted that Botrychium was reproduced only by adventitious buds.‡

These notions, however, are founded in an error, easily accounted for by the want of transparency of the tissue. This error consists in omitting to observe the very narrow points of junction of the cavities of the pairs of fronds as

* 'Flora,' 1839, p. 301.
† 'Vergl. Unters.,' p. 88.
‡ 'Die Pflanzenzelle,' p. 304.

well *inter se* as with the atmosphere, and with the (hitherto entirely unobserved)* depressed empty space above the vegetative centre or terminal bud of the stem.

The second and the third frond also of the germinating Botrychium are scale-like, of a whitish colour, and composed of elongated cells containing very little solid matter; nevertheless the second frond *sometimes*, the third *always*, have a greenish tip (Pl. XLII, fig. 9), which is the first indication of the lamina of the frond. In the fourth frond this green portion is more fully formed: it contains on either side two or three feathery flaps, between the lowest of which the rudiment of the fertile frond makes its first appearance in the form of a hemispherical protuberance. It produces only a few, usually two, simple ramifications. This pair of fronds, after breaking through the sheathing portion which forms the principal mass of the third frond, rises above the surface of the earth during the next vegetative period, and represents a diminutive moon-wort, not differing essentially from the older ones. It is not yet ascertained whether, during the subterranean growth of the germ-plant, one only of the scale-like fronds is developed yearly, as is the case with full-grown plants. It is very unlikely that such should be the case: the formation of the first, second, and third fronds probably takes place in the first vegetative period of the germ-plant, which consequently would develope in the second year the first green frond, and at the same time the first spore-bearing frond.

Each new pair of fronds makes its appearance near the almost smooth end of the stem of the full-grown plant in the form of a minute flatly-conical protuberance. The basal sheathing portion is first developed by active multiplication of the cells, especially in the direction of a plane passing through the median line of the organ and radial to the longitudinal axis of the stem, so that the rudiment of the pair of fronds destined to be developed in the third following spring covers the terminal bud of the stem, like the cotyledons of a liliaceous plant. The apex of the frond-

* This circumstance was not noticed by Presl and Mettenius, but was observed by Röper in a paper which appeared after the publication of the above observations. (See 'Bot. Zeit.,' 1859, p. 242.)

rudiment is at this time almost hemispherical, without a trace of a division. The fore-edge of the base of a frond is not in organic connexion with the tissue of the end of the stem upon which it rests; at this place there is a low but tolerably wide fissure (Pl. XLII, figs. 10^b, 11). In the second summer a flat cellular mass first makes its appearance out of the rounded apex of the frond-rudiment: this is the rudiment of the sterile frond, upon which the lowest pinnæ of the lamina first make their appearance. Whilst the next four, five, or six segments of the sterile frond are making their appearance on the continually-elongating end of the cellular body, (and frequently also at an earlier period), a button-shaped cellular protuberance becomes visible close underneath, and almost between, the oldest pinnæ of the sterile frond; this is the rudiment of the fertile frond (Pl. XLII, fig. 2). So far the pair of fronds is developed up to midsummer of the second year. The further development remains dormant until the following spring. During this time the transverse fissure which divides the fore edge of the sheathing base of the frond from the underlying tissue continues still open for a short space; it forms a direct communication between the hollow spaces which enclose the pairs of fronds for the second and third following years and the terminal bud. The transverse fissure first disappears during the vegetative period in which all the parts of the pair of fronds are completed,—twelve months before the final appearance above ground,—whilst the ramifications of the fertile frond proceed from the protuberance in front of the points of insertion of the lowest segments of the barren frond. The development, as in the barren frond and in the fronds of ferns, is centrifugal.*

Development of the vegetative organs of Ophioglossum vulgatum.—The thick covering of cellular tissue which sur-

* Röper has made an interesting observation ('Bot. Zeit.,' 1859, p. 257), viz., that plants of *Botrychium Lunaria* growing in loose sandy ground sometimes exhibit lateral ramifications on the subterranean stem, originating, it would seem, from the formation of adventitious buds underneath the base of the frond. The growth of these lateral branches resembles to a great extent that of germ-plants, inasmuch as at first they form scaly leaves only, and ultimately, when a leaf first appears above ground, fertile and barren segments are formed contemporaneously.

rounds the young undeveloped frond of Ophioglossum is not entirely closed. On that side of it which is turned towards the next older frond (which has broken out of its covering) it exhibits a narrow opening surrounded by a tuft of jointed hairs constituting in this plant the only appendicular organs of the epidermis (Pl. XLI, fig. 1). On the inside also the hollow space which covers the oldest of the enveloped fronds is not closed. A narrow cylindrical passage leads from its fore-side into the cavity which encloses the next younger frond, and from this in like manner into the cavity in which the frond destined for development in the third following year is produced; and lastly the latter is in open communication with the narrow space above the flat end of the stem (Pl. XLI, figs. 1, 2).

The fronds surround the end of the stem in a $\frac{2}{5}$ left handed spiral, as may be clearly seen in transverse sections of the stem at the place where the vascular bundle which passes from the cylinder of vascular bundles obliquely upwards to the fronds, traverses the cortical parenchyma (Pl. XLI, figs. 3, 3^b). The young frond makes its appearance near the depressed, almost flat end of the stem, in the form of a slender conical knob, from the fore side of which a fleshy flat stipule-like excrescence, as in Marattia, is produced (Pl. XLI, fig. 2^b). This cellular mass developes in breadth more vigorously than the part of the frond which is situated above its place of attachment. It embraces about two fifths, and the frond about one third, of the zone of the stem upon which they both stand. The axile stipule attaches itself by its fore edge to the front surface of the stipule of the obliquely-opposed next older frond and at its lateral edges it amalgamates immediately with the stipules of the adjoining older fronds to the right and left,* which stipules have already amalgamated *inter se*, and protrude considerably beyond the youngest frond behind which they stand. By this means the hollow space is formed which encloses the young frond. The walls of the cavity are derived from four different sources. The wall which is turned towards the front surface of the enclosed frond con-

* The second and third, reckoned backwards from the frond of which we are speaking.

sists, in its lower portion, of the hinder side of its own particular stipule, and in its upper portion, of the stipule of the next older frond. The greater part of the wall which is turned towards the hinder side of the frond, is composed of the front surface of the stipule of the third youngest frond, and the remainder of the latter wall is formed of the front surface of the stipule of the second youngest frond. The different stipules amalgamate at all points of contact with the exception of those points which are coincident with a line perpendicular to the apical cell of the stem. Consequently there remains a very narrow open canal leading to the apex of the stem into which the different cavities enclosing the fronds debouch by a small opening (Pl. XLI, figs. 1, 2).

If a careful section be made through that part of the stem in which the punctum vegetationis lies, the three-sided apical cell of the stem is seen at the base of the canal* leading to the punctum vegetationis, surrounded by the youngest secondary cells (Pl. XLI, fig. 4). Longitudinal sections through the terminal bud (Pl. XLI, fig. 2^b). exhibit most distinctly the deep depression of the apex of the stem into the prematurely developed peripheral tissue; a phenomenon which, here as elsewhere, depends upon an early vigorous diametral cell-multiplication accompanied by a very slight almost obsolete longitudinal cell-multiplication.

The course of the vascular bundles of *Ophioglossum* is simple; they form a cylindrical net, one of the meshes of which corresponds with each frond, and sends out to the frond a vascular bundle from its apical angle. Frequently, however, all the cellular tissue which fills up the meshes is transformed into scalariform vessels, so that the stem then, for considerable distances, exhibits a closed cylinder of vessels. Sometimes this condition is found only in one longitudinal moiety of the stem, whilst in the other the distribution of the meshes of the vascular bundles is the same as in the neighbourhood of buds. Roots—remarkable for the slight development of the root-cap—spring

* The canal is somewhat enlarged above the punctum vegetationis.

from the bundles adjoining the sides of the meshes of the reticulated vascular bundles of the stem; their position with regard to the fronds is not a definite one. *Ophioglossum vulgatum* (like *O. pedunculosum*), is often reproduced by root-buds. The new plant is reproduced by the multiplication of a cambial cell of the vascular bundle which traverses the longitudinal axis of the widely-creeping adventitious root, and is at first concealed in the cortical parenchyma of the root. However, this mode of reproduction is not so essential for the economy of the plant as in *O. pedunculosum*, a species which may be called monocorpous, inasmuch as its shoots usually die off when they have brought forth sporangia: its perennial duration rests, it may be said, exclusively upon the adventitious shoots of the roots.*

The appearance of fertile fronds on the front surface of the sterile ones is the same in Ophioglossum as in Botrychium, and justifies the same conclusion, viz., that the fertile frond is a shoot of the sterile one.

Mettenius has published some observations upon the germination of Ophioglossum ('Farrne des Leipz. Botan. Gartens,' Leipzig, 1856,' p. 119). He found the subterranean prothallia and germ-plants of *Ophioglossum pendunculosum* growing in the neighbourhood of the mother-plants. Artificial sowings of the spores were unsuccessful. The youngest prothallia which he found consisted of a small globular knob, of from $\frac{1}{2}$ to $1\frac{1}{2}$ lines in diameter, from which a conical prolongation of about two lines in length proceeded. The delicate-walled cells of the parenchymatal tissue of this knob were filled with amyloid granules: the superficial cells, and the capillary roots proceeding from them; were already dead. The formation of the knob was thus already ended, and the growth of the prothallium limited to the prolongation, whose cells filled with thick protoplasm, were in an active state of division. In older prothallia the prolongation attains a considerable length, as much as two inches. Its growth arises from the repeated division of a single apical cell by means of oblique septa. The daughter-cells ap-

* Like *Pyrola uniflora*. See Irmisch in 'Bot. Zeit.,' 1856.

peared in some prothallia to be arranged in three rows. Slender prothallia consist throughout, even in the cylindrical portion, of tissue homogeneous with that of the knob. In thicker prothallia a string of cells in the axis of the cylinder attains to double the length of the cells of the peripheral tissue. The former contain only a few amyloid granules; the latter are quite filled with them. Dichotomous prothallia were but rarely seen, and a repetition of the division of one of the branches was of still rarer occurrence. When in a normal position the apex of the prothallium tends to grow to the surface of the ground. As soon as it reaches the light it assumes a green colour, the amyloid granules receiving a covering of chlorophyll. The effect of light seems to be to limit the further growth of the prothallium: the protruding apex either dies, or becomes flattened, or divides into two or three small lobes, which develope themselves no further. Antheridia and archegonia are met with on the same prothallium without any definite number or arrangement. They are either altogether wanting on the knob, or are present in small numbers at the base of the prolongation. They are always plentiful upon the latter. Slender prothallia produce more antheridia than archegonia: in vigorous prothallia the archegonia are most numerous. The development of the sexual organs progresses from the base of the prothallium towards its apex. Their structure entirely resembles that of the same organs in Botrychium. The youngest observed embryos are ellipsoidal bodies consisting of few cells. That end of the rudiment of the embryo which is turned towards the apex of the prothallium forms the first leaf; the opposite end forms the first adventitious root. Both cause an expansion of the surrounding tissue; the leaf makes itself a passage for a longer or shorter distance into this tissue, sometimes penetrating, with a turn downwards, as far as the knob, and growing through it. After its egress the leaf is enclosed by the drawn-out portion of the prothallium. Its fore-surface is turned towards the apex of the central cell of the archegonium, a circumstance in which it agrees with Botrychium, and differs from the Polypodiaceæ and Rhizocarpeæ. The first root, as soon as it is formed, bends out-

wards, and pierces through the prothallium. Towards the base of the central cell of the archegonium the rudiment of the embryo is developed into a rounded inconspicuous swelling, consisting of wide cells filled with amylum. This swelling is the continuously-developing primary axis of the embryo.

CHAPTER X.

PILULARIA GLOBULIFERA AND MINUTA; MARSILEA PUBESCENS.

The fruit of Pilularia is the transformed end of a furcate branch, which is apparently produced in the axil situated between one of the long thin fronds and the principal axis, and which in *Pilularia minuta* is usually a lateral bud situated in one of the normal bifurcations of the stem. In *P. minuta* it forms when in the very young state, a globular mass of delicate homogeneous cellular tissue flattened at the apex. An outer layer of cellular tissue, composed of four layers of cells, surrounds two lenticular cavities which are separated from one another by a thick septum. The inner side of the outer wall bears the rudiments of sporangia. In this species, even at this early period of development, no traces of the junction of the amalgamated parts are visible at the apex of the fruit (Pl. XLIV, fig. 8). In the young fruit of *Pilularia globulifera* the commissures of the four delicate cross septa of the divided chambers exhibit very manifest lines of junction, which, in the half developed fruit (upon the outer wall of which numerous hairs are formed) are still unclosed. Here also clavate masses of cellular tissue, the first rudiments of the sporangia, spring out of the inner wall of the outer surfaces of these chambers. In *Pilularia minuta* there are only two or three of these masses, in other species as many as eight vertically one over the other. The wider end of the very young sporangia, which is borne by a short thick stem, exhibits a large central cell surrounded by a double layer of smaller cells (Pl. XLIV, fig. 3).

The central cell divides into two (Pl. XLIV, fig. 4), and each of the cells thus formed divides repeatedly into two cells turned towards all three directions of space. The cells of the two enveloping layers meanwhile divide only by septa perpendicular to the outer surface. The sporangium thus becomes a globular mass of large cells enclosed by a double layer of smaller tubular cells, and borne upon a very short cylindrical stem. The larger cells—the mother-cells of the spores—isolate themselves during the further growth of the fruit; the cells of the inner layer of the covering produce in the mean time numerous free small cells in their interior, which, as the membranes of their mother-cells divide, escape from the latter into the inner cavity of the sporangium (Pl. XLIV, fig. 5): at a later period they are absorbed. Each spore-mother-cell when it has become free divides contemporaneously into four daughter-cells which are the special mother-cells of the spores. This stage of development is attained at an earlier period by the lower sporangia than by the upper ones. After the walls of the special mother-cells have increased considerably in thickness, a spore is produced in each of them (Pl. XLIV, figs. 6, 10, 11). Up to this point all the sporangia behave alike. From this time however the further development of the lowermost sporangium of each compartment of the fruit differs very materially from that of the others. In the sporangium in question the special mother-cells and spore-cells (which are arranged in sets of four) all die slowly off except one (or two). The spores of the one set which remains soon become free by the absorption of the walls of the mother-and special-mother-cells, and assume a globular form. At first all four increase rapidly in size (Pl. XLIV, fig. 7); their walls then become much thickened but unequal-sided, so that the globular inner cavity of the young spore becomes excentric (Pl. XLIV, figs. 6, 11). The growth of one of the spores soon exceeds that of the others. The former alone continues to develope itself, whilst the growth of the others is arrested, and being pushed aside—like the remains of the mass of special mother-cells—by the one growing spore, they are soon dissolved. When the fruit is ripe the large spore occupies the

entire cavity of the sporangium, which in the mean time has become much enlarged. The shape of the spore changes during its growth from that of a globe into a short pear-like form (Pl. XLIV, figs. 12, 13, 14), and from the latter into that of an oval, slightly constricted at the equator (Pl. XLIII, fig. 1). In its narrow end, which is turned towards the apex of the sporangium, its nucleus is found embedded in a mucilaginous layer which clothes the wall.

By the time the spore has become globular a transparent outer membrane is distinguishable, differing from the delicate inner wall. Afterwards a second membrane, composed of prismatic closely appressed columnar cells, is formed upon this inner layer of the outer membrane. These columnar cells are very short at the base of the spore, much longer in its upper third part, but altogether wanting at the apical point of the spore. The ripe spore is clothed by a thick gelatinous layer, the component parts of which are also prism-shaped. This layer also does not cover the apex of the spore, to which there is access by a funnel-shaped passage through the gelatinous layer (Pl. XLIII, figs. 1, 7). The glassy inner layer of the outer membrane extends beyond the apex of the ripe spore in the form of a conical arch, open at the tip. It appears torn into numerous—in *Pilularia globulifera* as many as eight—three-sided shreds.

The spores which originated in the upper sporangia are transformed jointly and severally into much smaller globular spores, exhibiting at their apices three fissures of the exosporium, meeting at angles of 120°. These fissures point out the edges of contact of four spores inside a set of special mother-cells. In *Pilularia minuta* the small spores also are clothed with a gelatinous layer, which is wanting in those of *P. globulifera*. No trace of a nucleus is visible either in the large or small spores when ripe. The contents of both consist of a mass of albuminous fluid containing numerous firm granules of a substance rendered brown by iodine, as well as oil-drops and starch-grains. In the large spores the starch-grains, which are of a great size, exhibit manifest lamination, and a central cavity with fissures proceeding from it. In the

small spores the starch grains are exceedingly small and exhibit no structure.

The ripe fruit of *Pilularia globulifera* splits into four valves. The sporangia burst by the vast expansion of the internal jelly produced by the dissolution of the special mother-cells; the jelly becoming distended by the absorption of water. Numbers of large and small spores thus become free.

A few hours after this process the germination of the large spores commences. The first indication of this is the appearance of a lenticular agglomeration of finely granular protoplasm on the inner side of the apex of the spore, underneath the pyramidal arch formed by the triangular lobes of the inner membrane. This mass of protoplasm is soon clothed with a membrane, and then constitutes a very flat cell with a circular outline (Pl. XLIII, fig. 2). Shortly afterwards, before the expiration of twenty-four hours, the conical cavity formed by the lobes of the glassy layer of the outer spore-membrane appears to be filled by a cellular body, consisting of a large central cell surrounded by a simple layer consisting of a few tabular cells (Pl. XLIII, figs. 3, 3^b, 5). I did not succeed in finding the intermediate stages between this condition and the one previously described, but I do not doubt that this cellular body is produced by repeated bi-partition of the lenticular cell which is arched above. The lenticular cell may be first divided into four, by the production of septa cutting one another at right angles. It is probably one of these four cells, which—being divided by a diagonal septum inclined inwards—gives rise to the formation of the central cell, which latter cell growing more vigorously than the rest, soon occupies the middle point of the cellular body, and is covered by the other four cells which in the mean time have divided by septa perpendicular to the outer surface (Pl. XLIII, fig. 3). The central cell afterwards divides into a lower, flat, tabular cell, and an upper, spherical one. The lower tabular cell soon divides by repeated bi-partition into four (Pl. XLIII, fig. 5), then into eight, and afterwards into twelve cells. In the lower part of the prothallium thus formed, the cells which surround the sides of the larger central cell ultimately

divide by septa parallel to the outer surface (Pl. XLIII, figs. 7—9). The four cells which project beyond the apex of the larger cell expand above in a papillate manner (Pl. XLIII, fig. 5), after which each of them divides by a transverse septum (Pl. XLIII, fig. 4). All the cells of the prothallium, with the exception of these papillate cells and the large central one, form chlorophyll granules in their interior.

The increase in the circumference of the pro-embryo causes a bending back of the surrounding pointed shreds of the inner layer of the outer spore-membrane. The pro-embryo becomes visible in the form of an emerald-green wart at the apex of the germinating spore. The four papillate cells at the apex of the pro-embryo, and their four basal cells, now part asunder at the commissure, and thus an open canal, leading to the large central cell of the pro-embryo, is produced (Pl. XLIII, figs. 8, 9). Some of the papillate cells sometimes divide now by a second transverse septum (Pl. XLIII, fig. 9). A daughter-cell is in the mean time formed within the large central cell, the contents of which latter cell are finely granular and mucilaginous. This daughter-cell soon after its formation almost entirely fills the mother-cell (Pl. XLIII, figs. 8, 9). The central cell of the prothallium, and the four projecting cells, constitute the archegonium. The prothallium of Pilularia never produces more than one archegonium.

The development and structure of the prothallium of *P. minuta* entirely resemble those of *P. globulifera* as far as my observations extend, with the single exception that the base of the prothallium in the former is somewhat more strongly constricted than in the latter, so that the prothallium appears more spherical.

The small spores swell slightly after becoming free. The outer spore-membrane splits at the apex, forming three fissures, the direction of which corresponds to the edges of contact of the spore with the three sister-spores produced in the same mother-cell. The inner spore-membrane bursts, and some small spherical cells escape from the inner cavity of the spore; these cells contain small starch-grains and a lenticular vesicle attached to the wall (Pl.

XLIII, fig. 6). The lenticular vesicle encloses a very thin spermatozoon rolled up in three or four coils, which soon exhibits a rotatory motion in the interior of the enveloping cell. By rupture of the cell-wall it ultimately becomes free (Pl. XLIII, fig. 6*b*), and moves about in the water with helicoid contortions. Its fore-end, which is hardly thicker than the other, carries a few oscillating cilia (Pl. XLIII, fig. 6, *c—f*). I have observed the actual entrance of the motile spermatozoa into the mouth of the archegonium (Pl. XLIII, fig. 7).

A short time after the appearance of the spermatozoa in the neighbourhood of the large germinating spore, the large cell produced in the central cell of the prothallium appears divided into a few cells. The arrangement of these cells shows that their formation results from repeated division of the mother-cell by means of septa at right angles to a plane passing through the longitudinal axis of the archegonium (Pl. XLIII, figs. 10, 11). The cells of the prothallium, with the exception of the four papillate cells, multiply in the mean time actively in all three directions of space, especially the cells of the lower portion. Repeated division also occurs in the cells of the few-celled body enclosed in the prothallium, which body is the rudiment of the new plant, or embryo; and the result is, that the latter soon becomes a body composed of very small cubical cells, and having the form shown in Pl. XLIII, figs. 12, 13.

That end of the embryo which is turned away from the cavity of the large spore, and which points obliquely upwards, soon exhibits a more active development than is seen in its other parts. It is transformed into a cone which becomes continually more pointed as its development progresses. The multiplication of the cells is caused by continual division of the apical cell by differently inclined septa, and by the division of the cells of the second degree thus produced, by radial septa, and then by septa parallel to the longitudinal axis of the cone. The mode of cell-multiplication resembles in its essential features that of the first frond of the Polypodiaceæ (Pl. XLIII, fig. 15). A similar cell-multiplication, which at first, however, is very slow, takes place immediately underneath the place of origin of the

cone just mentioned (the first frond). Near it, at the opposite end of the embryo, a similar but shorter mass of cellular tissue soon begins to protrude (Pl. XLIII, fig. 15). This is the first root, an adventitious root, differing in no respect from those which afterwards appear in numbers. It grows, like the adventitious roots of the Polypodiaceæ and Equisetaceæ, by division of a cell in the interior of the tissue nearly underneath the apex of the organ. This division is produced partly by septa almost parallel to the basal surface, which is turned towards the apex of the root, and partly by septa parallel to the lateral surfaces which converge at an obtuse angle. The cells of the second degree which lie towards the apex of the root have the form of a meniscus; their first division takes place by a vertical septum bisecting the cell, after which a septum is formed cutting the one last formed at right angles. The four cells thus formed divide several times by longitudinal septa, but not by transverse septa (Pl. XLIV, fig. 2^c). The part of the root underneath the punctum vegetationis grows much slower than the part above it. Close above the punctum vegetationis the four outer cellular layers of the root separate from the two axile ones, and an annular air-cavity is produced. A similar air-cavity is formed in the first frond, even in its early youth (Pl. XLIV, fig. 1). The cells of the prothallium enclose the embryo on all sides even during the development of the first frond and the first root; they are much extended in the direction of the length of this organ, and gradually compressed and absorbed even up to the outermost layer. Contemporaneously with the first appearance of the root, the part of the embryo which is turned towards the large cavity of the spore, and separated from the latter by a simple cellular layer, becomes strongly concave (Plate XLIV, fig. 1). During the further development of the embryo it becomes more and more arched, until at last it has assumed the form of a short conical cellular mass enclosing an elongated pear-shaped cavity in connexion with the interior of the spore (Pl. XLIV, fig. 2). The cellular layer of the prothallium which encloses this cavity is afterwards dissolved. The distended portions of the proembryo which enclose the

first frond and the first root as it were with a sheath, are ultimately unable to keep pace with the growth of the latter. These portions are ruptured, and the apices of the frond and of the root become free. Almost at the same time the second frond appears near the place of origin of the first frond, and separated from it by the blunt end of the future principal axis: it has the form of a conical wart (Pl. XLIV, fig. 2), which by continual multiplication of the cells of its apex grows rapidly in length.

As the plant becomes further developed the joints of the stem elongate considerably: the terminal bud remains rather sharply conical. From the underside of the stem, in the immediate neighbourhood of the terminal bud, numerous bicellular hairs enclosing the latter are produced, and further backwards, close underneath the place of origin of each frond, adventitious roots make their appearance. The basal cell of the hairs which are situated on the outer wall of the fruit, divides repeatedly, at a late period and after the complete formation of the apical cell, by transverse septa; in this respect these hairs bring to mind the scales of the Polypodiaceæ.

The large oval ripe spore of *Marsilea pubescens*, at the time when it is discharged from the ruptured capsule, is of a similar nature to that of *Pilularia globulifera*. The inner cavity of the spore is clothed with a very delicate membrane, which becomes somewhat more manifest by distension, upon the application of caustic potash. In contact with this membrane there is found at first a tolerably thick glassy layer of a yellowish colour. Except at the apex of the spore—the spot, that is to say, which answers to the place of contact of the spore with its three sister-spores produced by the same cell—this glassy membrane is surrounded by an outer membrane, the component parts of which are prism-shaped, and arranged in a radial manner. Out of this outer membrane, and upon the apex of the spore, a portion of the middle membrane protrudes in the form of a blunt wart. The spore is enclosed in a thick layer of clear transparent homogeneous firm jelly, which extends beyond the apex of the spore almost throughout its entire length. An enlarged

passage leads through this gelatinous mass to the protruding portion of the inner spore-membrane. At the base of this passage are found the débris of the three sister-cells, which were produced in the same mother-cell with the spore. These are small shrivelled tetrahedral cells, which are attached by one of their points to the wart-like protrusion of the inner layer of the outer membrane of the spore (Pl. XLIV, fig. 16).

The inner cavity of the spore is filled with a fluid consisting of albuminous matter and yellow oil, and containing numerous large and small starch granules. The larger granules exhibit manifest lamination, and sometimes also indications of twin-granules. The protruding portion of the apex of the spore is separated from the rest of the cavity of the spore by a very delicate septum. It forms a distinct cell filled with a finely granular mucilage. When treated with caustic potash it exhibits in its middle point a nucleus of an ellipsoid shape (Pl. XLIV, fig. 18). This cell is the mother-cell of the prothallium.

Germination begins a few hours after the escape of the spore from the opening fruit. In the primary cell of the prothallium two new nuclei appear in the place of the primary nucleus which disappears (Pl. XLIV, fig. 17), and shortly afterwards the cell is divided into two longitudinal halves by a vertical septum. The longitudinal division is repeated in each half by a septum at right angles to the former one (Pl. XLIV, fig. 19). In the mean time an orange-red colouring matter appears in the mucilaginous fluid contents of the two or the four cells, in the form of small vesicles (or drops?) By a series of bipartitions the prothallium is transformed into a hemispherical cellular mass (Pl. XLIV, figs. 20—24), consisting of a central cell with mucilaginous contents, supported upon a double layer surrounded by a triple layer of narrow cells. The four longitudinal rows of cells which extend beyond the apex of the central cell, part asunder at their edges of contact, and an open narrow passage leading to that cell is formed (Pl. XLIV, fig. 22).

The structure of the prothallium of Marsilea consequently agrees in its essential features with that of Pilularia, except

that it is more massive, and differs from Pilularia in the subordinate point that the cells which form the mouth of the passage leading to the central cell do not become papillate. Here, as there, the entire prothallium is devoted to the formation of one archegonium.

The spores of Marsilea which came under my observation did not become further developed. The small spores procured contemporaneously from the same fruit,* which was $8\frac{1}{2}$ years old, exhibited no change: it would seem that these latter lose their power of germination sooner than the large spores. The prothallia died when they had attained the stage of development necessary for impregnation, inasmuch as the small spores mingled in the surrounding fluid developed no spermatozoa. I observed the same phenomenon in *Pilularia minuta*.

* For which I was indebted to the kindness of Alexander Braun. They were part of the same gathering which yielded the materials for his and Mettenius's observations, and were found at Montpelier in 1842.

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CHAPTER XI.

SALVINIA NATANS.

At the latter end of autumn the large ripe spores of Salvinia form ellipsoidal cells whose longitudinal diameter is from $\frac{1}{7}'''$ to $\frac{1}{5}'''$, clothed with a thick outer membrane in which two layers are visible, the inner one being horny, and the outer one granular and of a looser texture. At the apex of the spore—that pole of it which is turned away from the stalk of the sporangium—the outer membrane exhibits a division into three lobes, the boundaries of which answer to the edges of contact of the young spore with the three sister-cells which were produced contemporaneously in the same mother-cell.

The contents of the spore look like a quantity of oil and albumen. Spherical drops, both large and small, of a half fluid substance, swimming in a thinner fluid, fill the interior of the spore. The apical portion of it is occupied by a larger accumulation of the like mucilage. The history of the development of the spore, which when half ripe appears filled with delicate round vesicles, as well as the behaviour of the above spherical masses during germination, render it not improbable that some at least of those large drops are cellular formations filled with nutritive matter destined for the germ-plant.

During the winter the walls of the fruit perish. The sporangia—as well those which contain one large spore each, as those which contain small spores—fall from their stalks,

and are carried up to the surface of the water in the early spring by the surrounding growing masses of confervæ. In the last weeks of March a short three-edged cellular body of a beautiful emerald-green colour is seen at the apex of the spore, between the three separated lobes of the outer spore-membrane. This body is the prothallium.

The prothallium is produced by continued bi-partition of the agglomeration of granular mucilage which was spread over the arched apex of the interior of the spore, and has become transformed into a flattened cell (Pl. XLV, fig. 1). The prothallium whilst still very young is already multicellular, and exhibits a simple cellular layer, spread over the inner arcuate cavity of the macrospore (Pl. XLV, fig. 3). When seen from above it appears to have a bluntly triangular form (Pl. XLV, fig. 4). From the arrangement of the cells it may be concluded, that when the primary mother-cell was first divided by septa perpendicular to the membrane of the macrospore, a three-sided and a four-sided moiety were normally formed upon each division. As soon as the middle of the prothallium, by transverse division of its cells, has attained a thickness of three cellular layers, the first archegonium is formed at its apex. The position of the cells of the prothallium—which at this time is still entirely enclosed by the lobes of the spore-membrane and is devoid of chlorophyll—when seen in longitudinal section, shows clearly that this first archegonium was formed by transverse division occurring twice in the middle cell of the prothallium. The middle of the three daughter-cells becomes the central cell of the archegonium. At first it is much drawn out in width and is almost tabular (Pl. XLV, fig. 5). The upper cell first divides twice by longitudinal septa arranged crosswise. The four daughter-cells are afterwards, and after their free outer surface has become arched, divided by transverse septa (Pl. XLV, fig. 6). By parting asunder at their edges of contact they form the canal leading to the central cell. In the lower one of the three cells which are derived from the middle cell of the prothallium, the cell-multiplication which prevails in the entire mass of the prothallium is continued, and by this means the circumference of the latter is considerably enlarged, and thus—some time after the

formation of the first archegonium—the three lobes of the outer spore-membrane* are bent back.

The formation of the subsequent archegonia, which appear in numbers upon the prothallium, takes place in a similar manner by transverse division of one of the cells of the outer surface of the prothallium. The central cell is formed from the inner of the daughter-cells, whilst from the outer ones are produced the boundary cells of the canal leading to the central cell. After the formation of those archegonia, which are situated near the highest of the three blunt angles of the three-sided, cushion-shaped prothallium, transverse division is sometimes several times repeated in the covering cells of the archegonia, and in the tissue surrounding them. The canal leading to the central cell of these latter archegonia is of considerable length, and has a bent course (Pl. XLV, fig. 10).

At the commencement of the formation of the archegonium the central cell is quite filled with granular mucilage, and a nucleus with more transparent contents floats in the middle of it (Pl. XLV, fig. 5). Afterwards, as the central cell increases in size, the granular protoplasm accumulates so as to cover the wall, and the nucleus is imbedded in it. One or two oval or pear-shaped cells, in contact with the inner wall, are now visible in the upper arch of the cell: these are the germinal vesicles (Pl. XLV, figs. 6—9). They not unfrequently occur in pairs, a fact not hitherto observed in any other vascular cryptogam.

During these changes in the large spores, the sporangia which contain small spores are also carried up to the surface of the water, either in groups or singly. In autumn, when the mother-plant dies, the small spores contained in each ripe sporangium are firmly attached to one another and not capable of isolation, their outlines being hardly distinguishable. This has been observed by Mettenius,† and the same is the case even in early spring. If however such a sporangium be subjected at this time to gentle pressure under

* The two glassy inner layers remain during this process, as during the entire act of germination, quite unchanged (Pl. XLV, fig. 2). The notion of their conversion into an apparently cellular mass is erroneous. (Mettenius 'Beitr. z. K. d. Rhizocarpeen,' p. 17.)

† 'Beitr. zur K. der Rhizocarpeæ.' Frankfort, a. M., 1846, p. 19.

the microscope, spherical or elongated ellipsoidal cells may be seen to escape from the fissures between the cells of the wall as they part asunder. These spherical or ellipsoidal cells are divided by delicate septa into from two to six compartments, filled with finely granular mucilage, in which one or several nuclei float. Afterwards each compartment contains from one to four free roundish cellules. Each of these cellules encloses a spiral thread, a spermatozoon, which after its escape by the rupture of the wall of the cellule moves about actively in the water. Many of these cellules —those namely which are less developed—contain, instead of the spiral thread, a transparent vesicle (or nucleus?) in the centre, in the interior of which dark spherical lumps of mucilage (nucleoli?) are sometimes visible. By careful dissection of microsporangia under the microscope at the beginning of March, I succeeded in separating entire the inner cell membranes of the microspores from the glutinous contents of the microsporangia, which consisted of the detached and agglomerated exosporia of the microspores. When isolated they appeared in the shape of cellules already extended to an oval form, having a major axis of 17·5 m.m.m., with turbid granular contents, and a spherical transparent nucleus (Pl. XLIV, fig. 26). In the latter half of March the contents of the microsporangia are pultaceous: the cellules lie free in the granular mucilage of the interior, which is brownish green under transmitted light. By this time the contents of the cellules are transparent, and most of them are divided transversely (Pl. XLIV, fig. 5). Further divisions lead to the formation of a multicellular oval body, the antheridium, in the compartments of which the spermatozoa are formed in the interior of spherical vesicles (Pl. XLIV, figs. 27—30). By using higher powers of the microscope, it may be seen that the cilia of the spermatozoa, which are less numerous than in the Polypodiaceæ, are of unusual length (Pl. XLIV, figs. 31, 32). The movements of the spermatozoa are exactly like those of the spermatozoa of the Polypodiaceæ, so far as regards the direction and the rapidity of the motion.

I have several times in different years found spermatozoa of this kind swimming about in the water in which Salvinia

had germinated. There can be no doubt that in the regular course of nature, they are set free from the microsporangia by gradual decay of the walls of the latter.

In archegonia which die without being impregnated and become brown, the remains of the germinal vesicle are still visible, and of their original size. Those archegonia however which by the widening of the central cell and the multiplication of the cells adjoining to the latter give evidence of impregnation, exhibit a considerable increase in size of the germinal vesicle, which now almost fills the central cell (Pl. XLV, fig, 9).* As soon as it quite fills the central cell, the first division of the impregnated germinal vesicle takes place, by means of a transverse septum slightly inclined to the longitudinal axis of the archegonium. Cross longitudinal septa are produced in each of the two halves, and then again slightly inclined transverse septa are formed. The succession of these divisions is not subject to any definite rule (Pl. XLV, figs. 11—14): the final result however is always the same, viz. the formation of an oval cellular body having its longitudinal axis at right angles to that of the archegonium, and having one of its apices, the blunter one, composed of four cells placed crosswise (Pl. XLV, fig. 14^c), whilst the other apex only exhibits a single top cell (Pl. XLV, figs. 13, 14^b, 15^c). I will call the latter the fore-end, and the former the hinder end of the embryo.

At the hinder end the number of the cells increases almost uniformly in all directions (Pl. XLV, figs, 19, 21, 23). At the fore-end on the other hand a particularly active cell-multiplication occurs, which commences in the growing cell adjoining the original apical cell of the pointed end of the embryo. This cell-multiplication is produced by septa inclined alternately forwards and backwards, and at right angles to a plane passing through the longitudinal axis of the archegonium and of the oval embryo. In this way an excrescence originates which is directed upwards (Pl. XLV,

* I did not succeed in observing spermatozoa in the interior of these archegonia. A phenomenon which has been observed in different mosses and in *Pteris aquilina* occurs, as an irregularity, also in Salvinia, viz., that the interior of the archegonium enlarges more rapidly than the imperfectly developing embryo, which is thus surrounded by a wider cavity (Pl. XLV, fig. 12).

figs. 21—23,) and which becomes rapidly wider by longitudinal divisions,* first of the apical cell, and then of the other cells of the fore-edge (Pl. XLV, figs. 20, 24,) of the flat and leaf-like structure. This excrescence is the first leaf.

Soon after its appearance, a shoot of the fore-end of the embryo is observable underneath its place of attachment and before its median line. This shoot appears at first as a hemispherical, slighty protuberant, cellular excrescence. The arrangement of the cells of the embryo, especially if observed in a longitudinal section through the median line of the first leaf (Pl. XLV, fig. 21), leads to the conclusion that the excrescence was formed by the division of the apical cell of the fore-end, first by a septum inclined towards the first leaf, and then by a septum inclined in the opposite direction.† These divisions are repeated in regular succession in the terminal cell for the time being, which cell has the form of a segment of a sphere. This excrescence is the principal axis of the germ plant. On the right and left of it the margin of the lamina of the first leaf is developed into ear shaped appendages (Pl. XLV, figs. 24, 25^{a-c}). Whilst these—extending beyond the end of the principal mass—approximate more and more nearly to one another, the still leafless apex of the leafy shoot ramifies twice, sending out the more slender ramification (normally) first to the right and then to the left‡ (Pl. XLV, fig. 25^{a-c}). In the mean time the cells of the hinder end of the embryo only multiply to a small extent. That end is now attached at right angles in the form of a stalk-like prolongation, to the flat, proportionably thick, first leaf, which forms the principal mass of the embryo (Pl. XLV, figs. 22, 26, $25^{a,b,c}$). Its cells are now throughout almost cubical.

This growth of the first leaf ruptures the prothallium (Pl. XLV, fig. 26). By the expansion of the cells of the hinder end of the pro-embryo,—which expansion takes

* These divisions are interpolated between the divisions produced by septa inclined to the outer surfaces.

† The succession of the division may be inverted (Pl. XLV, fig. 19).

‡ The observer is supposed to look from above upon the fore-surface of the first leaf.

place suddenly and at right angles * to the surface of the first leaf—the first leaf and the principal bud are carried upwards out of the fissure (Pl. XLV, fig. 27). The stalk-like organ which bears the first scutiform leaf is therefore not formed exclusively, or even mainly, by the longitudinal extension of either the lower end of the embryo which lies opposite to the entrance to the archegonium, or of the primary axis, which in Salvinia is only very slightly developed: The hinder end of the embryo plays the principal part in the formation of the above-mentioned stalk.

The vascular bundles originate from the stalk. Nevertheless, the interior of the latter does not produce any spiral vessels which pass immediately into the first leaf and the stem above it (Pl. XLV; fig. 28); here all the cells of the bundle remain thin-walled. The second and the third leaf are formed behind the ramifications of the principal bud, without the occurrence of any new ramifications (Pl. XLV, fig. 28, 29). Then, however, the less vigorous branches become elongated (usually ramifying again at the same time), and form the leafless branches, of limited growth, which hang down into the water, and which have been generally considered by the earlier writers as adventitious roots.† These branches grow by the repeated division of an apical cell by means of septa, inclined alternately in two directions, and by the division of the cells of the second degree by a radial longitudinal septum, and then by a transverse septum perpendicular to the axis. Afterwards the cells divide, by septa parallel to the axis, into inner and outer cells, and this latter division is several times repeated in the cells of the circumference.

I observed myself—what Savi had previously noticed—that microspores which had been carefully kept apart from microsporangia developed a prothallium, but no embryos. It is but rarely that two embryos are produced in the same prothallium. I have only observed the occurrence twice.

The Rhizocarpeæ have always attracted a considerable

* This direction forms an angle of about 30° with the longitudinal axis of the embryo.

† Mettenius has correctly described them, 'Beitr. zur Botanik.,' Heft i, (Heidelberg, 1850) p. 15.

amount of attention from botanists, especially their germination.* The knowledge of them had progressed considerably when Schleiden's well-known work threw the whole subject into confusion.† Schleiden alleged that the small spores (pollen-grains, as he called them) emit a tube, which penetrates into the prothallium developed from the large spores, and is there transformed into the embryo. Schleiden made these statements with a positiveness which would have admitted of no contradiction, had it not been for some almost unaccountable errors of observation. Mettenius, in his beautiful and accurate work, 'Beiträge zur Kenntniss der Rhizocarpeæ,' did not venture to attack this theory of Schleiden, although he was unable to verify any one of Schleiden's observations. Nageli ‡ never saw the small spores of Pilularia emit tubes, but he made the important discovery that the mother-cellules of the Spermatozoa originate in them. He pointed out anew that the four papillate cells of the mouth of the archegonium—which Schleiden, strange to say, described as "pollen grains seated upon the nucleus, and which had developed tubes"—could not be pollen-grains, but that they rather originated from the prothallium. I published the outlines of the account given above many years ago.§ Mettenius, in a subsequent work, adopted my views.‖

* The earlier literature is fully treated of in Mettenius's work 'Beiträge zur Kenntness der Rhizocarpeen,' Frankfurt a. M., 1846, p. 1.

† 'Grundzüge,' 2nd edition, p. 101.

‡ 'Zeitschrift f. Botanik,' Heft 3 and 4, (Zurich, 1846,) p. 188.

§ 'Bot. Zeit.,' 1849, No. 45.

‖ 'Beitr. zur Botanik,' 1 Heft, Heidelberg, 1850.

CHAPTER XII.

ISOETES LACUSTRIS.

The development of the Isoeteæ is a subject of great importance in botanical morphology. They are the only known family in which the principal axis never ramifies. As far as present observations extend, they alone, in the vegetable kingdom, are distinguished by the entire suppression of a supplementary cell-multiplication in the joints of the stem. In other stems, however little their internodes may be developed, an active multiplication of the cells in a longitudinal direction takes place (after the formation of the youngest internode) in the second youngest, or even in the adjoining internodes. In Isoetes, after the formation of one internode, the longitudinal growth terminates absolutely. The features by which the Isoeteæ are clearly distinguishable from the plants nearest allied to them in their mode of reproduction are as follows:—the development of adventitious roots (apparently in a descending series), the form of the ligneous mass, and especially the existence of a mantle of cambium surrounding the wood and retaining its activity during the whole life of the plant. The processes of impregnation are seen in Isoetes with greater facility and clearness than in any other diœcious cryptogams.

Hugo von Mohl pointed out the peculiar phenomena of growth of the Isoeteæ,* viz., the development of the adventitious roots in an apparently descending order on both sides of a furrow traversing the under surface of the

* 'Linnæa,' 1840. 'Vermischte Schriften,' p. 122.

flattened stem—the peculiar form of the wood—and the annual renewal of the bark by the vitality of a cambium layer surrounding the wood. Since Von Mohl's discoveries the special attention of botanists has been almost constantly directed to this interesting family. Alexander Braun * pointed out the connexion between the $\frac{1}{2}$ or $\frac{2}{3}$ arrangement of the fronds of young plants, and the two or three-lobed form of the stem; he discovered the true nature of the regular bifurcation of the roots, which had been taken by earlier observers † for accidental lateral ramification. He endeavoured to explain the remarkable relation of the roots to the stem by the assumption that "the roots in Isoetes, instead of breaking forth outwardly from the vascular cylinder, penetrate, on the contrary, in an inward direction." Mettenius,‡ about the same time, gave a very accurate account of the structure of the ripe spore, and suggested that the germination of Isoetes might agree with that of Selaginella, as to which,§ at the same time, he published the first correct microscopical observations. A year afterwards, Karl Müller gave an account of the germination of *Isoetes lacustris*.‖ He describes the large spore (of which he had only advanced specimens before him) as a cellular sac, enclosed by an exosporium, and in whose cavity the rudiment of the embryo appeared in the form of a free cell, which was gradually transformed into the cellular body. Mettenius forthwith corrected the most essential errors of this account.¶ He proved anew, in a striking manner,** the similarity of the germination of Isoetes and the other vascular cryptogams, by the discovery of the formation of spermatozoa in the small spores, and the description of the origin of the archegonia upon the prothallium developed by the large spores.

The following observations will afford some facts supplementary to those noticed by Mettenius and Müller,

* 'Flora,' 1847, p. 32.
† Bischoff, 'Krypt. Gewächse,' Nürnberg, 1828, p. 10.
‡ 'Linnæa,' 1847, p. 269, on Azolla.
§ l. c., p. 270, note.
‖ 'Bot. Zeit.,' 1848.
¶ 'Bot. Zeit.,' 1848,' p. 688.
** 'Beitrage zur Botanik.,' Heft 1, Heidelberg, 1850.

and will be found in accordance with those reported by Mohl. I am indebted to the kindness of Mettenius,* Alexander Braun, and Gustav Reichenbach,† for the abundant materials upon which my observations are founded.

The large spores of *Isoetes lacustris* are at first tetrahedral with a convex *basal* surface. As they ripen, their remaining surfaces also become gradually arched, and assume almost a spherical form. The delicate primary cell-membrane is clothed with a thick exosporium, which, when cut through, exhibits three principal layers. The innermost is a glassy membrane, of a brown colour and moderate thickness, upon which ridges of different lengths, and converging towards the pole of the spore, are seated. Three of the longer and more prominent of such ridges, answering to the edges of contact of the spore with its three sister-spores, unite at the apex at angles of 120°. They reach to the equator of the cell, and there intersect a somewhat less prominent annular ridge, which surrounds the spore. This innermost layer of the exosporium is succeeded by a thinner layer, of a granular consistence and yellowish colour, over which the thick outermost covering, consisting of a transparent gelatinous mass, is spread. Like the former one, it covers all the ridge-like protuberances of the innermost glassy layer of the exosporium, and it is especially fully developed over the four principal ridges (Pl. XLVI, fig. 1).

The matter composing the exosporium behaves towards reagents like the exine of pollen-grains. Sulphuric acid imparts a reddish colour to the inner layers, which are softened by boiling in alkaline leys. The gelatinous layer is rapidly destroyed by mineral acids and caustic alkalis. As Röper‡ has observed, the exosporium does not contain carbonate of lime, although Schleiden§ suspected its presence from the appearance of the dry spores. The contents of the ripe spore in its optical and chemical characters

* I received living specimens of *Isoetes lacustris* from the lake in the Black Forest, the same habitat which afforded the materials for the observations of Bischoff, Mohl, Braun, and Mettenius.

† Dried specimens of species of the Mediterranean Flora.

‡ 'Zur Flora Mecklenburg's,' vol. i, p. 125.

§ 'Grundzüge,' 2nd edit., vol. ii, p. 84.

resemble a mixture of oil and albumen. If a spore be crushed upon thin paper, it leaves behind a transparent stain.

A few weeks after the spore has become free by the decay of the walls of the sporangia, its interior begins to be filled with cellular tissue. Sections afford no explanation as to the nature of this cell-formation. If a spore which is not yet entirely filled with closed parenchyma be crushed, its contents become a formless pultaceous mass. If however the exosporium be immersed for half an hour in a saturated solution of glycerine, it becomes sufficiently transparent to expose to view flatly-spherical accumulations of a granular substance spread over the inner wall of the spore (Pl. XLVI, fig. 1). There can be no doubt that these masses of granular mucilage, which become confluent when the spore is submitted to pressure, are newly-formed primordial cells, *i. e.*, naked primordial utricles; and therefore that the formation of the cellular tissue which fills the spore, *i. e.*, of the prothallium, is the result of free cell-formation. This accords with the mode of origin of the endosperm of the greater number of phænogams, and especially with the development of the albumen of the Coniferæ. The formation of rigid cell-membranes appears to commence for the first time when the accumulated contents of the spore-cell have become transformed into daughter-cells.

This cell-formation probably commences in the apical arch of the spore-cavity. When the parenchyma of the spore is sufficiently firm to admit of longitudinal sections, the cells of the apex of the prothallium are far smaller and more numerous than those of its base. This leads to the conclusion that a multiplication of the cells has commenced at the apex some time previously, which multiplication does not take place at the base until a much later period, and then with far less activity. The contents of the cells of the prothallium are not distinguishable from those of the ripe spore. No nuclei are visible in the thick turbid fluid.*

During the formation of the prothallium the inner mem-

* The want of transparency of the milky cell-contents is so great, that even in very thin sections it prevents the recognition of the boundaries of the cells as long as the preparation lies in clean water. The addition of concentrated solution of glycerine produces with greater rapidity a far more perfect transparency than the chloride of calcium recommended by Mettenius, ('Beitr. zur Bot.,' Heft i, p. 11.)

brane of the spore changes considerably, especially in its upper portion. It increases in thickness, and when a section is made, several layers are distinguishable. It can with difficulty be stripped off from the prothallium.* When viewed superficially the membrane which was previously homogeneous appears finely granular—all which phenomena are found to occur in a remarkably similar manner in the embryo-sac of the Coniferæ.

The spherical prothallium increases in size by multiplication and expansion of its cells, and ruptures the upper half of the exosporium, dividing it into three lobes, each of the three ridges which unite at the apex of the spore separating into two longitudinal halves. A small portion of the apex of the prothallium—three very pointed triangles meeting at angles of 120°—is thus made free.

Archegonia are produced by the multiplication of individual cells of the upper surface of these exposed portions. The first of these archegonia is produced exactly at the apex of the prothallium (Pl. XLVI, fig. 2). If this first one remains unimpregnated several others are formed in descending order. I have never counted more than eight.

The mother-cell of an archegonium divides by a septum parallel to the free outer surface, and a similar division takes place in the outer of the two newly-formed cells. Vertical longitudinal septa then divide each of the two upper cells into longitudinal moieties (Pl. XLVI, fig. 3*a*), in each of which a longitudinal septum at right angles to the one last formed is immediately produced. The undermost cell of the archegonium increases somewhat in size and becomes the central cell. Division by transverse septa usually occurs once more in the lower of the two double pairs of (four times smaller) cells which project beyond the central cell (Pl. XLVI, fig. 3, a^1). Exceptions to this are rare.

During these processes the part of the inner membrane of the spore-cell which is not covered by the exosporium peels off gradually, swelling up in front.† By the parting asunder of the four longitudinal rows of cells which cover

* Compare Mettenius, 'Bot. Zeit.,' 1848, p. 690.

† The mode of growth of the adventitious roots of some grasses, especially of *Avena sativa*, affords a very remarkable instance of the peeling off of whole masses of cellular tissue by the casting off of the primary membrane and the thickening layers of the epidermal cells.

the central cell of the archegonium, an open passage is formed leading to the latter cell (Pl. XLVI, fig. 5). Before the formation of this passage a free spherical daughter-cell is produced in the central cell, almost filling the cavity of the latter (Pl. XLVI, figs. 4—6). It is the primary cell of the new generation—the germinal vesicle—capable, after impregnation by the spermatozoa produced in the small spores, of forming a new frond and spore-bearing plant of Isoetes.

All the ripe macrospores of *Isoetes lacustris* form prothallia and produce archegonia. The further development which results in the formation of the embryos of a leaf-bearing plant is attained only by those macrospores which come in communication with microspores. This is analogous to what occurs in Selaginella and the Rhizocarpeæ. Prothallia when kept quite apart from microspores live for a long time; according to my experiments from the beginning of September to the middle of March. Some of these even then brought forth new archegonia of the normal form apparently fitted for impregnation.

The small spores of *Isoetes lacustris* when ripe have the form of the quadrant of a sphere; in rare instances they are tetrahedral. The sharp edges and angles of the spore are formed of exine, those of the inner spore-membrane are bluntly rounded off. At both the upper and lower ends of the spore the exosporium forms a wart-like tip (Pl. XLV, figs. 8, 9); all along the edges of contact of the spore with the three sister-spores it forms a prominent fold (Pl. XLVI, fig. 7). The outer surface of the exine is very finely granulated, almost smooth. Its colour is a light yellowish grey.

The fully-developed small spore contains a finely granular protoplasm mixed with many small oil-drops. When viewed with transmitted light the mass of differently refractive fluids appears almost opaque. A sharp-outlined spherical nucleus with transparent fluid contents floats in the middle point of the spore (Pl. XLVI, fig. 7).

About four weeks after the microspores have become free by the decay of the wall of the sporangia, the primordial utricle of the cell divides into from two to four portions which become individualised into daughter-cells (Pl. XLVI, fig. 8).

Sometimes the moieties of the primordial utricle fill the mother-cell entirely; the cell-walls secreted by them then appear—so far as they correspond with the surfaces of contact of two halves of the primordial utricle—like septa seated upon the inner wall of the spore (Pl. XLVI, fig. 9).* More frequently however the division of the cell-contents is accompanied by a contraction† of them into a smaller space; the daughter-cells, which are of a flatly ellipsoidal form, lie free in the interior of the spore. Numerous very small amyloid granules now appear in the fluid contents of the daughter-cells. Each of these cellules produces in its interior one or two lenticular vesicles, in each of which is produced a thread, rolled up in a right-handed spiral, and consisting of a substance rendered brown by iodine (Pl. XLVI, fig. 11). One of its ends is somewhat thickened, the other is drawn out into a thread-like termination. When perfect, the spore and its daughter-cells are ruptured by the swelling of the contents; the lenticular mother-vesicles of the spermatozoa become free in the opened cavity of the spore. Soon the membrane of the vesicle itself—which is rendered blue by iodine—is ruptured; one end of the spermatozoon protrudes from the fissure, and immediately commences an active oscillatory motion, which causes a rapid revolution of the mother-vesicle (Pl. XLVI, fig. 12). Ultimately the spermatozoon frees itself entirely from the vesicle, and the turns of the spiral separate somewhat from one another. It slips out of the ruptured spore, maintaining a constant revolution round the axis of its spiral, and moves about in the water with the thick end in front, dragging the thinner one after it (Pl. XLVI, figs. 13—15). Its motions are slightly more rapid than those of the spermatozoa of mosses.‡

If the spermatazoon be killed with iodine, a small number

* Spores thus divided are exactly like the small ellipsoidal cellular bodies which burst forth in the spring from those sporangia of *Salvinia natans* which produce microspores, *i. e.*, the cellules in whose chambers the mother-vesicles of the spermatozoa originate.

† Analogous to the process occurring in the spore-formation of liverworts and mosses (Pellia and Phascum).

‡ Mettenius, who discovered the spermatozoa of Isoetes, remarks upon the slowness of their motion compared with the rapid motion of the spermatozoa of ferns.

of very fine cilia attached to the two front coils of the spiral may be distinguished under favorable illumination (Pl. XLVI, figs. 16, 17). The addition of colouring matter to the water in which the spermatozoa are moving, shows that during the life of the latter these cilia oscillate actively. The duration of the motion of the spermatozoa of Isoetes never exceeds three hours according to my observations.

Microspores sown at the end of August produced the first spermatozoa in the middle of September. The production of spermatozoa lasted until January. The water of the vessels in which I. sowed the large and small spores, swarmed with spermatozoa on some days in the middle of October. At this time the thinly-fluid mucilage which fills the canal of the mouth of ripe archegonia, often contained thread-like bodies of a firm mucilaginous substance, which might be the remains of spermatozoa, whose motion had ceased.

The first indication of the commencement of the development of an embryo in an archegonium, is the division of the impregnated germinal vesicle by a transverse septum, somewhat inclined to the longitudinal axis of the archegonium (Pl. XLVI, figs. 18, 20). During the formation of this septum the germinal vesicle expands, often to some extent, in a direction at right angles to the longitudinal axis of the archegonium. After the disappearance of the primary nucleus of the cell and the appearance of two new nuclei, the lower of the two halves of the impregnated germinal vesicle, and afterwards the upper half also, is divided by a septum cutting the first formed septum at a right angle (Pl. XLVI, fig. 21). The rudiment of the embryo of the new generation, when consisting of from two to four cells, has the form of a procumbent oval; when viewed in the direction of its longitudinal axis (Plate XLVI, figs. 18, 19), it appears not longer than the unimpregnated germinal vesicle. But owing to its longitudinal expansion, it has already began to penetrate destructively into the tissue of the prothallium.

As in many similar cases, the cells of the prothallium which immediately adjoin the rudimentary embryo, exhibit a somewhat active multiplication before they become

loosened and pushed aside by the developing germ-plant, and ultimately dissolved.* The embryo in its first stages appears surrounded by a tissue of very narrow cells (Pl. XLVI, fig. 21). As early as during the occurrence of the first divisions of the impregnated germinal vesicle, the cells of the mouth of its archegonium die; their fluid contents become as clear as water, and their walls assume the deep-brown colour so common in the dead cell-membranes of vascular cryptogams. Similar changes sometimes occur in those cells of the upper surface of the prothallium which adjoin the mouth of the archegonium (Pl. XLVI, figs. 21, 23).

It very rarely happens that more than one archegonium of the same prothallium is impregnated. The rest wither; the contents of their central cells shrivel up into an irregularly shaped ball of dark-brown matter, and all the cell-membranes of the archegonium become brown.

The rudiment of the embryo when 4-celled grows towards the middle point of the spherical prothallium by repeated division of the cells turned away from the canal of the archegonium. At the same time an active multiplication commences in the one lateral cell which occupies the more pointed end of the oval embryo-rudiment. It divides by a vertical septum forming an acute angle with one of the axes of the embryo. The outer of the newly-formed cells is immediately divided again by a septum at right angles to the last-formed septum. In the apical cell for the time being of the excrescence (of the embryo) thus produced, the division is repeated for a long time by septa inclined alternately in two different directions (Pl. XLVI, figs. 22, 23). This lateral shoot of the young rudimentary plant—which shoot up to a certain point is continually elongating—is the first leaf.

The cells of the second degree produced by the division of the (primary) apical cell of the leaf, are divided by radial longitudinal septa. Each of the tertiary cells divides—

* Instances of this occur in the development, whilst within the prothallium, of the germ-plant of ferns—in the penetration of the lower end of the moss-fruit into the incipient vaginula—and in the displacement of the endosperm of many phænogams by the growing embryo.

by septa parallel to the chords of the arched free outer surfaces—into an inner and an outer cell. In the latter a septum is produced at right angles to the one immediately preceding it, and radial to the longitudinal axis of the leaf; close under the growing tip of the leaf eight peripheral cells enclose four axile ones. The form of the leaf, which at first is flattened above and below, is gradually changed by this cell-multiplication into a conical one (Pl. XLVI, fig. 24). The leaf increases in thickness by repeated division of the cells of its circumference, produced by radial longitudinal septa alternating with septa parallel to the tangents of the free outer walls. When it has attained a certain stage of development its longitudinal growth is much accelerated by the occurrence of transverse division in most of its cells. This multiplication commences close underneath the apex of the leaf, and progresses from thence, on the one side towards the base, and on the other side towards the apex, so far at least as it extends into those cells of the apex of the leaf which have been formed since its commencement. The cells of the circumference divide first; from the latter the multiplication proceeds towards the longitudinal axis, without reaching the four rows of cells adjoining the latter. The latter remain twice as long as the cells of the peripheral layer; they are destined at a later period, by repeated longitudinal divisions, to become transformed into vascular bundles (Pl. XLVII, fig. 1).

The first leaf either shoots out at right angles from the longitudinal axis of the archegonium and embryo, or it trends upwards, often at such an acute angle that its apex penetrates into the upper arch of the central cell of the archegonium. The latter case is the most frequent; it very rarely happens on the other hand that the leaf takes a downward direction towards the centre of the prothallium.

As early as the time when the number of the cells of the leaf, counted in a longitudinal direction, amounts to from four to six only, the free outer wall of the cell which occupies the middle of the base of the upper surface of the leaf—that surface which is turned towards the apex of the prothallium—begins to swell in a vesicular manner (Pl. XLVI,

fig. 23). The protuberance has the form of an ellipsoid flattened on the upper and under side, and is separated from the original cavity of the mother-cell by a septum (Pl. XLVI, fig. 24). The roundish cell, not unlike a knobby hair, which is now seated at the base of the fore side of the leaf, is the primary cell of the single scale which it produces. Its first divisions exactly resemble those of the cell of the first degree of one of the gemmæ of Marchantia or Lunularia. The cell is divided two or three times by transverse septa, which are at right angles to the future longitudinal axis of the scale, and perpendicular to its surfaces (Pl. XLVII, fig. 1). The apical cell then divides, and after it the lower cells also, by a longitudinal septum at right angles to the one previously formed. The halves increase—after new transverse septa have been formed in each of the two upper cells—by the growth of septa parallel to the free outer edges of the scale, followed by septa produced in the outer of the newly formed cells at right angles to the outer margin. The organ which has now the shape of a blunt spatula (Pl. XLIX, fig. 4), continues to increase the number of its cells by the division of those of its circumference by means of longitudinal and transverse septa which alternate with tolerable regularity. This activity of the cells terminates much sooner at the apex of the leaf than at its base, where an intercalary multiplication of the cells occurs, mainly in a longitudinal direction, some time after the cells of the apex of the leaf have lost their power of division. The scale becomes pointed and heart-shaped (Pl. XLIX, fig. 5).

All these septa are perpendicular to the surfaces of the scale. Soon, however, septa parallel to its surfaces appear in its middle cells (Pl. XLVII, fig. 2). Thence the division advances towards the cells of the base of the leaf, which are engaged in intercalary multiplication in length and breadth. In the cells nearest to the base the division is sometimes repeated, so that this part of the scale consists of three layers. The remainder of it has two layers, with the exception of the margin and the top, which always exhibit a single layer of cells. Individual cells of the margin grow out into rather long pointed papillæ.

In all the principal features the development of the scale of Isoetes accords with that of the scales of ferns. The first commencement of the multiplication of the single primary cell is essentially the same in both, *i. e.*, it rests upon the alternation of rectangular, longitudinal, and transverse divisions; besides this, both exhibit the subsequent intercalary basal cell-multiplication, and the same kind of multiplication of the median cellular layers; and lastly, in both cases the development of the scales rapidly gets ahead of that of the organ to which they form appendages, and they soon die.

Immediately after the commencement of the formation of the scale, a sheath begins to be formed at the base of the leaf, enclosing the scale and some of the cells underneath it. A horse-shoe-shaped, cushion-like protuberance, open towards the front surface of the leaf, is first formed by the arching outwards of the free outer wall of a girdle of cells surrounding those parts (Pl. XLVII, fig. 24). When the intercalary cell-multiplication of the base of the leaf takes place, this protuberance grows up into a tolerably high annular sheath, by repeated division of the apical cell for the time being by means of horizontal septa (Pl. XLVII, fig. 2).

The leaf grows in thickness at the point of origin of the scale; its fore-side appears bent obliquely inwards (Pl. XLVII, figs. 2, 3), close above the base (Pl. XLVII, figs. 2, 3). In its lower part, the vascular bundle which traverses it is excentrical, being nearer to the front surface.

The primary axis of the germ-plant, which at the time of the appearance of the first leaf consisted of only a few cells, increases considerably in length and circumference during the development of the leaf and the formation of its scale. This increase is caused more by expansion than by multiplication of its cells. The axis now projects considerably from the embryo, in a hemispherical form, and is directed towards the middle point of the prothallium; the leaf is seated upon one of the lateral surfaces of the embryo (Pl. XLVI, fig. 24; Pl. XLVII, figs. 1-3).

A process of cell-multiplication has now commenced upon its opposite lateral surface also: this is the beginning

of the formation of the first root, an adventitious one, like all the roots of the vascular cryptogams. Its development commences with the multiplication of a cell of the inner tissue of the embryo, viz., the cell which lies opposite to the primary cell of the first leaf, and is separated by a cellular layer from the upper surface of the germ-plant (Pl. XLVII, fig. 1). This cell divides, in repeated succession, by transverse septa opposite to one another, forming cells of the second degree, lying alternately above and below the primary cell. The lower ones are produced by the formation of a septum slightly convex below; their form is that of a meniscus. Their multiplication takes place in two directions only; all the septa which are formed in them are perpendicular to the arched upper and under surface of the cell whose derivative cells constitute one of the cap-shaped cellular layers—enclosed one within the other—which cover the outermost apex of the root, and which, during the growth of the latter, gradually peel off outwardly (Pl. XLVII, fig. 3). After the formation of a lower secondary cell, and before the division of the cell of the first degree by a septum opposite to the last-formed septum, septa parallel to the longitudinal axis of the root are produced in the latter cell three times in succession. One of these septa is turned towards the outer side of the root—that side which is turned away from the punctum vegetationis of the germ-plant. The two other septa are at right angles to this one. Thus three lateral cells of the second degree are formed, which are followed by the production of a shorter upper cell by the division of the primary cell by means of a transverse septum (Pl. XLVII, fig. 3). I will call the first three the outer, the second the inner of the upper secondary cells. Both kinds of upper cells of the second degree, the lateral cells as well as those which follow them, multiply in all three directions. Their divisions are oftener repeated and last longer than those of the lower secondary cell which belongs to the same period of division of the primary cell.

The formation of lateral cells of the second degree causes a very considerable unilateral thickening of the root. The diameter of the latter increases much more rapidly on

that side which is turned away from the future place of origin of the second root, than on the opposite side. The consequence of this is that each new cap-shaped covering layer of the tip of the root appears to be attached more obliquely than the preceding one, and reaches higher up on that side of the root which is turned towards the punctum vegetationis than it does on the opposite side.

Each newly-formed inner cell of the upper cells of the second degree is first divided into unequal longitudinal portions by a septum inclined inwards to the axis of the root, the inner portion, that, namely, which is turned towards the punctum vegetationis of the germ-plant, being the smaller one. Both portions multiply immediately in all three directions. The two innermost cells which adjoin the longitudinal axis of the root, and are turned towards one another, remain about one step behind all the others in the process of division by transverse septa, *i. e.*, by septa at right angles to the longitudinal axis of the root. Instead of that division they each divide twice by longitudinal septa at right angles to one another. Thus there is produced within the root a string of sixteen longitudinal rows of extended cells, situated excentrically, being nearer to the inner side. This is the rudiment of the vascular bundle (Pl. XLVII, fig. 3). The cells of the outer surface of that portion of the root, which,—as opposed to the root-cap which peels off little by little—may be called the persistent portion, divide by radial longitudinal septa and by transverse septa once oftener than those of the inner surface; the epidermis of the root consists of tabular cells four times smaller than those adjoining them on the inside. These divisions of the cells of the outer surface occur even within the region which is protected by the transient cap-shaped covering layers of the tip of the root; they occur on the outer side of the root, where these coverings do not extend so high up, earlier (*i. e.*, nearer to the tip of the root) than on the inner side (Pl. XLVII, fig. 3).

Some of these circumstances attract but little attention in the first root of the germ plant which is hardly as thick as a bristle, in consequence of the inferior development of the tissue destined to form the bark of the root. In order

to explain them I must speak, in anticipation, of the process of development of vigorous roots of plants some years old (Pl. LII, figs. 2—5).

The one cell which is situated underneath the place of insertion of the scale of the first frond, and is surrounded by its sheath-like base, is the punctum vegetationis of the (secondary) principal axis of the plant; the terminal bud of the embryo is at this time limited to this one cell. As the bud is developed the cell divides by septa inclined alternately in opposite directions. The lines in which these septa cut one another are at right angles to the front surface of the first leaf.

Until the plant is fully formed the growth of the stem is caused by the constantly repeated uniform division of the apical cell. The direction of the septa produced in it remains always the same, viz., at right angles to the major axis of the ellipsoidal transverse section of the stem, and parallel to the furrows of its under side.

The mode of multiplication of the cells of the second degree which are thus produced, resembles in general that of the same cells of the first leaf above described. After the formation of the second secondary cell, the second leaf is produced on that side of the end of the principal axis which is turned away from the first leaf, by the multiplication of the youngest cell of the second degree of the stem-bud. The mode of its development corresponds entirely with that of the first (Pl. XLVII, figs. 2, 3). Its formation commences immediately after the first root becomes visible; during its development the upward growth of the surrounding sheath of the first leaf ceases for some time. When the second leaf has attained a height of from three to four cells, a remarkable elongation of the cells of the first leaf—which now contain chlorophyll—commences at the apex of the latter. In consequence of the multiplication of its cells in a longitudinal direction, the first leaf has by this time advanced almost to the periphery of the prothallium. The leaf breaks through the prothallium and appears in the form of a green point outside the latter: it elongates itself very rapidly by the longitudinal expansion of its cells, which proceeds from the apex of the leaf towards its base, where cell-multiplica-

tion is still in progress. In my experiments the first leaves broke out from the ends of the prothallia at the end of September, six weeks after the spores were sown. From that time leaves continued to make their appearance singly until the middle of January, when their number suddenly diminished in a remarkable manner. From the beginning of February until towards the end of March no new germ-plants became visible; at the commencement of spring however they began to appear again, becoming continually more numerous until the middle of April. Even in the middle of May almost all the prothallia which I examined contained embryos in different stages of development. These prothallia were surrounded by the episporium, and had been produced from a sowing made in the middle of the preceding August. Such was the result of chamber culture. It is probable that in the natural condition the embryos which break through the prothallium in winter do not survive, and that those germ-plants only which are produced in spring attain to a further development.

Soon after the appearance of the first leaf, the first root also breaks through the prothallium. It bends itself downwards and penetrates into the mud, the leaf having a vertical direction, inasmuch as being specifically the lighter portion of the plant it stands erect in the water. The prothallium is now attached laterally to the embryo. The thin mass of cellular tissue at its apex forms a ring round that portion of the germ-plant between the root and the front surface of the leaf. The large-celled blunt end of the primary axis of the young plant extends into the principal portion of the prothallium, whose cell-contents, like those of the cells of the first axis of the plant, henceforth become gradually transformed into a transparent fluid.

After the breaking through of the leaf and the root, the further development of the germ-plant ceases for about a month. Expansion and multiplication of the cells of the first leaf and of the first root still continue, taking place in the former by intercalary multiplication of the cells of the base of the leaf, in the latter by the growth of the apex. But the formation of new leaves and new roots goes on only slowly and gradually.

The above-mentioned two-fold longitudinal division of the string of elongated cells which become differentiated in the interior of the leaf and root does not occur until after the latter have emerged from the prothallium. The divisions appear to take place contemporaneously throughout the entire length of both the cellular strings which unite underneath the terminal bud. The division by transverse septa of the basal cells of the leaf, continues even after the commencement of the formation of the vascular bundle, although in a less degree; and the cells of the string which goes to form the vascular bundles take part from time to time in the division. One single longitudinal row of cells is entirely exempt from it. This row originates in the middle of the fore side of the vascular bundle, by supplementary longitudinal division of a row of cambial cells. In the cells of this row, whose length—owing to the entire suppression of all transverse division—far exceeds that of all the neighbouring cells, thickened annular threads soon make their appearance, passing here and there into spiral threads (Pl. XLVII, fig. 3). The continual longitudinal growth of the surrounding tissue stretches and distorts the young vessel, and removes the annular threads to a considerable distance from one another.

In like manner there appears on the inner side of the rudimentary vascular bundle of the root a row of elongated spiral and annular cells of a prosenchymatal form like the vessels of the leaf. In the first node of the plants, at the place where the precursors* of the vascular bundles of the leaf and root unite underneath the rudiment of the second leaf, more than one of the longitudinal rows of cambial cells assume a prosenchymatal form, and thickenings of the walls are formed in all of them (Pl. XLVIII, fig. 1). These cells, which are the first rudiments of the wood, are short and spindle-shaped,† and already bear some resemblance in form to the cells of which the principal mass of the wood of the mature plant will consist.

Many of the cells of the tissue which adjoins the vascular

* Précurseurs *Mirbel.*

† The intercalary transverse division has not extended to the cells adjoining these.

bundles of the leaf and of the root separate at their edges, and the intercellular cavities become filled with air. The tissue which is filled with air soon dries up; at last it disappears altogether, and large air-cavities are formed;—four cylindrical cavities parallel to the axis are formed in the leaf, and are divided into a series of compartments by persistent cellular surfaces; in the root one large air-cavity is formed in front of, and near to the excentrical vascular bundle.

Whilst the base of the second leaf begins to form a sheath round the terminal bud, the latter produces the third leaf at a point opposite to the second, and above the first (Pl. XLVII, fig. 3). At the same time the formation of the second root commences. It originates under the second leaf, opposite to the first root, very near to the first node, and is produced by the multiplication of a cell adjoining the string of cells which goes to form the vascular bundle. It is formed in precisely the same manner as the first root, with which it makes an angle of about 30° opening downwards. A plane passing through the longitudinal axis of the first and second leaves and of the first root, usually bisects the second root also; small lateral deviations are however not uncommon. The root in its longitudinal development stretches the outermost cellular layer of the rudimentary stem of the germ-plant to a considerable extent before it breaks through it (Pl. XLVII, fig. 3).

The rudiment of the third root, like that of the first and second, only becomes visible when the third leaf has already attained a certain degree of longitudinal development. It is produced, like the second, by the multiplication of a cell adjacent to the lower end of the precursor of the vascular bundle, and to the rudimentary ligneous body of the germ-plant, and originates consequently on the left hand, close above the place of origin of the first root. In its development it turns itself at once somewhat sideways; it makes its way through the cortical tissue of the stem of the germ-plant in a direction which diverges about 30° laterally from that of the first root.

The fourth and the following leaves, at least as far as the

eighth, exhibit the $\frac{1}{2}$ arrangement.* The commencement of the formation of each new leaf takes place some time before the cessation of the growth (*i. e.*, the cell-multiplication of the base) of the next preceding one. The lowest part of the back of the leaves enters into the formation of the bark of the stem, like the base of the underside of the leaf of the Equiseta, the Lycopodiaceæ, and the phænogams. The $\frac{1}{2}$ arrangement of the leaves causes an excessive increase in the mass of the cortical tissue at two points of the circumference of the stem lying opposite to one another, and corresponding with the dorsal surfaces of the leaves. Here the bark is developed so as to form two fleshy bodies widened at the base,† and spreading obliquely downwards from the ligneous body of the stem. These bodies are separated from one another by a flat indentation which is at right angles to the large horizontal axis of the stem, and is the first rudiment of the characteristic furrow of the underside of the stem.

The development of each young leaf, and the growth in thickness of its base, proceed *pari passu* with the cell-multiplication in circumference and diameter, of the older portion of the end of the stem, as well as of the base of the preceding leaf by which the young leaf is sheathed. The active increase in the number of the cells round the upper end of the longitudinal axis, pushes the previously formed portions of the circumference of the stem continually further outwards. The latter are able to bear this pressure for a long time by the expansion of their cells in a tangential direction. But in the plane which passes through the small horizontal axis of the stem this expansion is almost entirely suppressed. At this part the cortical parenchyma splits from the outside (sideways and from below), at an early period, by which means the furrow of the under side of the stem is made much deeper.

Shortly after the commencement of the formation of each new leaf, a new root is produced laterally beneath it; the

* As Alex. Braun remarked in 1847 ('Flora,' p. 135), and which he pointed out as the immediate cause of the bipartite arrangement of the stem of Isoetes.

† This widening is due to the greater vigour of each new leaf.

fourth being near to the second, and obliquely opposite to the third. The primary cell of the fifth root lies near the first, exactly opposite to the third. The sixth originates near the second obliquely opposite to the fifth. The places of origin of the roots of the first year—as well as of all the successive periods of vegetation—consequently all lie in a plane passing through the indentation of the underside and the terminal bud of the stem. The roots are developed in ascending order. Each new root originates somewhat higher up, and farther from the longitudinal axis of the stem than the second preceding one, *i. e.*, its next neighbour underneath. The points of origin of the roots of the first vegetative period form together an arc slightly convex below (Pl. XLIX, figs. 1, 1^b). During the development and the penetration through the bark of the roots subsequent to the third root, the former are compelled (like the third root itself), to bend downwards towards the furrow* of the stem, in order to avoid the vascular bundles of the preceding roots. If the third root diverges to the right of the longitudinal axis of the elliptical transverse section of the stem, then the fourth will turn to the left of it, the fifth also to the left, the sixth to the right, and so forth. Each new root converges at a more acute angle to the small horizontal axis of the stem; the last roots of the first year are almost parallel to that axis and to the furrow of the underside of the stem (Pl. XLVIII, fig. 5).

The roots as they break through the bark bend sharply downwards, and appear on the underside of the stem arranged in two rows almost parallel to the indentation of the latter. The locus of the points of penetration of the roots may be considered as forming an elongated ellipse.† The roots which are nearest to the centre of the stem and the lowest down, are the oldest, those which spring from the wide lateral margins and are the highest up, are the youngest. The vascular bundles of the third and following roots, which are excentrical like those of the first and second, are brought near to that side of the root which is turned towards the furrow of the stem; the excentricity

* This furrow becomes continually more and more clearly defined.

† Von Mohl, 'Vermischte Schriften,' p. 127.

is reckoned not with reference to the longitudinal axis of the stem, but to a plane passing through this axis and the indentation of the stem, in which plane the points of origin of the roots are situated.

The tissue of the region of the stem in which the closely crowded horizontal places of origin of the vascular bundles of the leaves meet together, goes to form the upward-growing portion of the proportionably slight woody mass which occupies the longitudinal axis of the stem, but encloses no pith.

In the germ-plant, as long as the $\frac{1}{2}$ arrangement of the leaves lasts, this upper half of the woody mass has a two edged form. Its usually spindle-shaped cells—reticulated and spiral cells mixed with a few delicate walled cells—have almost all the same direction; they are parallel to the larger transverse diameter of the woody mass (Pl. XLVIII, figs. 2, 3; Pl. XLIX, fig. 1^b). A longitudinal section through the furrow of the stem cuts all the wood-cells transversely. As the arrangement of the leaves passes through the $\frac{1}{3}$ into the $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, and $\frac{8}{21}$ arrangements, the upper part of the woody mass becomes round, and the direction and form of its cells very various, appearing at first sight to have no regularity, owing more particularly to the fact that now many other cells besides the primary cells of the vascular bundles take part in the wood-formation. Spiral cells are also formed which are situated between the converging rudimentary portions of the vascular bundles; by this means the woody mass is closed up to the form of a cylinder.

The closely crowded points of origin of the roots represent the under half of the woody mass: a row of spiral cells concave above, at right angles to the larger horizontal axis of the upper mass of wood, which latter in the first year is two-edged.

At the close of the first vegetative period of the germ-plant the cells of the bark are filled with amyloid granules, mixed with a few oil-drops. The cells, however, which immediately surround the mass of wood retain their capacity for multiplication. Some time before the commencement of the first period of winter-rest they have divided

once, twice, or three times by septa parallel to the longitudinal axis of the wood. Thus there is formed a mantle of cambium surrounding the mass of wood on the sides and from below, and passing above into the growing cellular tissue of the end of the bud.

At the recommencement of vegetation in the second year an active multiplication of the cells of this cambial layer begins. The increase in size keeps pace with the growth in thickness of the new portion of the stem produced by the development of the terminal bud. The multiplication of the cambial cells is most remarkable at the sides of the mass of wood; it is less vigorous in that half of the cambium which surrounds the lower, half-moon-shaped portion of the woody mass.

The development of the cambium has pushed outwards the cortical tissue which is filled with assimilated matter. The vascular bundles are thereby much stretched, but not so as to destroy them. The vitality of the cells of the vascular bundles manifestly still exists; by the expansion of their own walls they follow the change of position of the surrounding tissue. The thickenings of the walls of the vessels are alone materially changed during these processes, being loosened here and there and in other places distorted, so that every trace of regular arrangement disappears (Pl. LXI, fig. 3). The function also of the vascular bundle does not seem to have come to an end at the time of the commencement of the vegetative period which succeeds its formation. The starch and oil contained in the cells of the bark of the previous year—which bark has been pushed outwards—are gradually sucked up and carried to the growing portions of the plant. At the end of each vegetative year the cells of the bark of the preceding year contain only a transparent fluid.

The old bark which is pushed outwards, gradually dies from the periphery inwards; its cell-walls assume a deep brown colour, and ultimately the bark perishes. The new bark behaves similarly to the old bark, in the fact that the cells of the portion which clothes the furrow of the stem only expand slightly in breadth. The indentation of the stem already appears deeper than in the preceding year, on

account of the less active development of the corresponding region of the bark-forming cambium, and it becomes deeper still by the regular tearing away of the tissue of the bark from the sides, that tissue not being stretched transversely.

The roots of the previous year are pushed for some distance outwards and downwards with the bark through which they have penetrated. Like the latter they assume a deep brown colour and die.

The new roots destined for the support of the plant during the current period of vegetation originate on the convex edge of the lower, half-moon-shaped portion of the mass of wood, by the multiplication of some of the cambial cells adjoining the wood. The nature of their cell-multiplication corresponds in almost every respect with the account given above of the first root. The only difference is that during the passage through the bark the transient cellular layers of the root-caps are inordinately developed, and the permanent cortical layer of the root, on the other hand, very slightly so.

The first root of the second year is formed close under the place of origin of the first root of the germ-plant, at the spot where the development of the cambium has torn off the vascular bundle of the root about to be cast off—*i. e.*, at the place of attachment of the latter root. The second root originates underneath the place of insertion of the second root of the previous year, the third under that of the third root of the previous year, and so forth. In their direction also the new roots agree entirely with the older ones. The two first originate opposite to one another, trending away from the lateral surfaces of the lower growth of wood, and bent in different directions *inter se*. They break forth opposite to one another in a perpendicular direction underneath the terminal bud, on both sides of the furrow of the stem. The third and following roots bend more and more sideways. The two last pairs of roots of one period of vegetation traverse the bark almost parallel to the furrow of the stem. All the roots as they grow through the bark describe a flattened arc concave to the indentation of the stem. A longitudinal section taken through that indentation lays bare within each half of the stem only the rudiments and

the tip of the older of the roots which are still hidden within the bark: the middle portion of the root is bent away from the plane of the section (Pl. LI, fig. 1).

As in the first year so also in the following ones the bark is pierced by the new roots close under the deepest part of the indentation. The brown roots of the previous year stand far outside those of the current year. Inasmuch as many of them last for two, three, or four years before they become quite decayed, the result is that in some plants, especially the older ones, the peculiarity observed by Von Mohl makes its appearance with the greatest distinctness. This peculiarity is, that the oldest roots are the outermost and apparently the highest, the youngest the innermost and apparently the lowest. As appears from what has been said above, this is only an *apparent* irregularity, depending upon the unusually vigorous development of the bark, and its yearly renovation from within outwards.

It is a rule without exception that the middle ones of each series of generations of roots are the oldest, that those which are nearer to the lateral terminal points of the furrow of the stem break forth at a later period than those in its middle point. This circumstance however is not unfrequently less striking, owing to the fact that the duration of each root is far less strictly limited to any definite period than that of the leaves. The outermost roots of the preceding series are almost always in a state of vitality when the first innermost ones of the next series begin to appear. Old vigorous individuals which form a large number (as many as twenty) of leaves in the course of one year, develope during this period *two* complete series of generations of roots; the whole cycle, commencing with the lowest innermost roots and progressing to the outermost, is formed twice in succession (Pl. LI, fig. 1). In the Isoetes from South Europe and North Africa, which produce an abundance of roots, as many as six generations of roots are produced in the same vegetative period. With the close of each cycle of roots a double pair is added to the number of the roots of the previous year, which double pair originates at the horns of the half-moon-shaped lower portion of the mass of wood (Pl. LI, fig. 1).

The position of the vascular bundles of the roots remains throughout the whole life of the plant the same as in the first year: they are always brought close to that side of the root which is turned towards the indentation of the stem. The cambial cells between the places of origin of those vascular bundles which pass to the new roots become for the most part woody: individual cells only, situated between the transformed annular and spiral cells, remain thin-walled (Pl. LII, fig. 6). Thus the latterally compressed lower half of the woody mass grows downwards at its convex edge, at the same time increasing in diameter.

The roots of Isoetes usually ramify in a furcate manner repeatedly—as many as four times—during their longitudinal development.* Judging from the arrangement of the cells of roots which have only just become forked, it would seem that the furcation commences with the longitudinal division of the cell of the first degree of the apex of the root, by means of a septum at right angles to the larger transverse diameter of the downward-growing wood (Pl. LII, fig. 2). The forks of the roots separate from one another at an angle of about 30°; the two first are parallel to the furrow of the stem. The direction of the next ramifications differs by about 90° from the former. The excentrical vascular bundles of the forks of the root are always removed to that side which is turned towards the sister-fork of the root (Pl. LII, fig. 3).

Every year the same processes are repeated. The old bark is thrown off and replaced by new. The upper cylindrical portion of the wood grows upwards by the lignification of those cells of the terminal bud which overlie its summit, and by the addition of the rudiments of vascular bundles intended for the new roots. Its half-moon-shaped lower portion increases in circumference on the convex edge, by the addition of the bases of the vascular bundles which pass to the new roots. Thus the plant becomes continually more vigorous; the number of the leaves and roots increases in each new vegetative period.

The abundant development of leaves, in connexion with

* Discovered by Alexander Braun in 1847. 'Flora,' p. 33.

the entire suppression of intercalary cell-multiplication in the joints of the principal axis, leads necessarily to the result that the younger portion of the bark formed out of the confluent basal portions of the leaves projects far beyond the punctum vegetationis of the principal axis. The top of old plants exhibits a remarkable funnel-shaped depression, upon whose inwardly-inclined slope the younger leaves which sheath one another are seated (Pl. LI, fig. 1; Pl. LII, fig. 1). The terminal bud occupies the base of the crateriform depression, exhibiting a blunt cone of cellular tissue (Pl. L, figs. 1, 2), surrounded at moderate distances by the rudiments of the youngest leaves, which in plants of from five to eight years old have the $\frac{5}{13}$ arrangement.

The nature of the cell-multiplication of the terminal bud remains (as has been said) the same throughout the entire life of the plant. The alternately oblique septa by which the apical cell divides in repeated succession, are inclined to the large lobes of the bark; a plane passing through the furrow of the stem cuts those septa at right angles. The daughter-cells of the cells of the second degree soon divide by transverse septa, and become cells of the third or fourth degree (Pl. LI, figs. 1, 2). Close under the apex of the terminal bud the arrangement of the cells, which at first was ladder-like, is changed into a concentrical scale-like arrangement. The inner cells—those nearest to the axis of the stem—of the derivatives of the third- and fourth-youngest cell of the second degree, expand remarkably in width in a direction radial to the longitudinal axis of the wood. By this means the terminal bud, even above the place of origin of the youngest leaf, is quite flattened (Pl. L, figs. 1, 2).

The effect of the yearly renovation of the cambial layer is not only to increase and renew the cortical tissue, but new spiral cells also become added, although only sparingly, to the wood of old vigorous plants. Individual cells of the cambium, separated by two or three cambial cells from the older principal mass of the wood, often exhibit thickenings of the walls, which by their delicacy and want of colour betray their undoubtedly recent origin (Pl. LI, fig. 2). New elementary organs are never added to the oldest portions of the wood, those namely which are formed in the one

and two-year old germ-plant: the two-edged lower end of its upper part retains its form unchanged during the entire life of the plant (Pl. LI, fig. 1; Pl. LII, fig. 1). The formation of new wood around that already present seems only to last during a few vegetative cycles. All longitudinal sections of plants from three to eight years old exhibit a somewhat exuberant enlarged growth of the wood close under the upper end. This locus of the greatest thickness of the wood consequently moves continually upwards during the development of the plant.

The primary portions of the vascular bundles which passed off into the leaves and roots formed many years previously, and which portions are attached to the wood, are compressed by the cambium surrounding their sides, which is always in a state of active vitality. Ultimately these portions are torn off and pushed outwards, and the stump which adjoins the mass of the wood is grown over by the cambium just in the same manner as the stem of a tree gets rid of the boughs of its lower portion.

The vigorous leaves of plants of many years' growth exhibit in their earliest stages, when viewed in front, the ladder-like arrangement of their cells (Pl. LII, fig. 7) which is the necessary result of the mode of multiplication of the cell of the first degree. This however soon becomes indistinct by the rapid and vigorous development of the leaf in thickness. The form, when viewed from above, of leaves which are somewhat more developed (Pl. LI, fig. 5) leads to the conclusion that now, after each two divisions by septa at right angles to the fore and hind surfaces of the leaf, septa are formed in the terminal cell at right angles to the lateral surfaces of the leaf and turned towards its front or hind side.

Isoetes lacustris exhibits a manifest periodicity in the interchange of sterile and fertile leaves.* In the terrestrial species this interchange is very striking. Microscopical investigation shows that the rudiments of the leaves are formed a full year before they are developed; the fruit-bearing ones being produced late in summer and in autumn, and the sterile ones in spring and early summer. During

* Described by Alexander Braun in the 'Flora,' 1847, p. 34. But see Bischoff, 'Krypt. Gewächse,' p. 84.

the winter the development of the leaves is considerably retarded, but does not entirely cease. Those leaves which are first formed in winter and make their appearance at the end of the next autumn, are very imperfect. In the scanty development of the leafy portion, and the vigorous development of the base, they form the transition to the stipule-like organ which in the terrestrial Isoetes, especially *I. Durieui* and *Hystrix*, appear at the commencement and the close of every vegetative period.* In the semi-terrestrial species such as *I. velata* and *adspersa*, the last leaves of the year exhibit—in a more marked manner than *I. lacustris*—a distorted leafy portion and an overgrown sheathing portion whose cells are quite filled with starch and oil.

The scales of the first leaves only of the germ-plant originate immediately above the place of attachment of the leaf. With the second leaf frequently, with the third and following ones always, the case is different. Here the cell which by the vesicular protrusion of its outer wall lays the foundation of the scale, is removed by at least one cell from the base of the leaf (Pl. XLVII, fig. 3; Pl. XLIX, fig. 1^b). The intercalary cell-multiplication of the base of the leaf takes place with remarkable activity in this one cell and in those cells which lie in the same horizontal plane. By this means the scale is carried upwards to some height on the leaf (Pl. L, figs. 1, 2; Pl. LIII, figs. 2, 3). A flat three-sided cellular mass then sprouts forth from the leaf close under the scale and covering the base of the latter (Pl. LIII, figs. 2, 3). Beyond and over the sides of this cellular mass the two lower angles of the triangular scale are developed in a downward direction; the base of the scale becomes heart-shaped like the scales of the Polypodiaceæ (Pl. XLIX, fig. 5). The cells of the base, which are inserted in the tissue of the leaf, exhibit a vitality which forms a marked contrast to the early cessation of the growth of its free portion. The horizontal row of cells produced by the multiplication of the first cell of the second degree belonging to the scale—which cell is enclosed by the substance of the leaf—is transformed by a series of rapidly repeated divisions into a transversely-extended ellipsoidal cellular body, the two ends of which, by

* Alex. Braun, in 'Exploration Scientifique de l'Algerie,' Pl. 36, fig. 1^b, 2^b.

repeated multiplication of the cells, ultimately grow upwards in such a manner that the base of the scale becomes a fleshy mass of very small cells with turbid contents, having the form of a horse-shoe opening upwards, and inclined inwards to the longitudinal axis of the leaf. Underneath also the exuberant growth of the base of the scale extends into the three-sided shoot of the front surface of the leaf, partly pushing forward the existing cellular tissue (Pl. LIII, fig. 5). As the longitudinal development of the leaf draws to a close, those of its cells which adjoin the highly-developed base of the scale become ligneous by spiral thickenings of the walls. Almost all the cells of the interior of the ligule-like shoot of the fore-side of the leaf take part in this wood-formation* (Pl. XLIX, fig. 1). In an upward direction it is only the one cellular layer adjoining the place of insertion of the scale which is transformed into spiral cells; on the other hand the whole of the tissue enclosed by the two horns of the half-moon-shaped base of the scale becomes woody. The middle of the lower end of the woody mass which is produced at a late period reaches close to the axile vascular bundle of the leaf.

The leaves of *Isoetes lacustris* which are formed in the third year after germination, and are developed in the fourth year, produce the first fruit. The rudiment of the sporangium † is formed in the earliest youth of the leaf, at the time of the commencement of the intercalary multiplication of its base. Of the two cells into which—by a tranverse septum—the cell underneath the place of insertion of the scale is divided, the upper one becomes the

* First observed by Mettenius, 'Linnæa,' 1847.

† Schleiden, out of love for some supposed analogies with the lower cryptogams, will only apply the term "sporangia" to the spore-mother-cells of the mosses and vascular cryptogams. Like most other botanists, I use the term "sporangia" for the fruit containing the spore-mother-cells and spores, for the capsules of mosses and liverworts, for the fruit of ferns and Lycopods, and for those portions of the fructification of the Equisetaceæ and Rhizocarpeæ which immediately enclose the spores. I do so because the term "sporangium" was first applied to the fruit of ferns. It appears neither necessary nor advisable to use the same term for the Fungi, Lichens, and Algæ, as is used for the Characeæ, mosses and vascular cryptogams. Moreover the expression "sporangium" is quite unnecessary in the case of the lower cryptogams. Descriptive botany already possesses a more than sufficient number of suitable names for the organs in question.

primary cell of the ligulate process which covers the base of the scale, and the lower one becomes the primary mother-cell of the sporangium (Pl. LIII, fig. 1). By repeated divisions in all three directions, especially in a longitudinal direction, the latter is soon changed into an oval hillock of cellular tissue, whose longitudinal axis coincides with that of the leaf (Pl. LIII, figs. 2, 3). The longitudinal and transverse divisions produced by septa perpendicular to the front surface of the leaf, are more active in each of the new outer cellular layers of the rudiment of the fruit, which are formed by septa parallel to the free outer walls of the cells of the upper surface. The young sporangium soon becomes an oval cellular mass attached to the leaf by a proportionably small basal surface. The tissue of the leaf which adjoins the place of attachment of the sporangium afterwards—when spore-formation begins—overgrows the fruit on all sides, principally above; it forms a membranous border, reaching far above the sporangium, and is the *veil* of descriptive botanists (Pl. LIII, fig. 5).

Until shortly before the appearance of this last growth of the base of the leaf, the sporangium consists throughout of homogeneous delicate walled cells, which now begin to be differentiated into three different sorts of tissue. The two outermost cellular layers assume more and more a tabular shape, and become the capsule wall. The interior divides into groups of delicate-walled cells in close connexion with one another—the primary mother-cells of the spores—and into plates separating these groups of cells from one another, and formed each of two layers of cells whose intercellular cavities contain air. The cells of the wall of the sporangium, as also those of the tissue destined to produce the reproductive cells, continue to multiply by division for some time longer. The cells of the plates which divide the portions of that tissue from one another keep pace with the increase in size of the sporangium by expansion of their walls (Pl. LIII, fig. 4).

At last the spore-mother-cells separate from one another, and assume a globular form (Pl. LIII, figs. 6, 7, 8). In the sporangia intended to form small spores, more generations

of spore-mother-cells are produced than in those which form macrospores; the spore-mother-cells of the latter are considerably larger. The spore-mother-cells, both after and before their individualization, exhibit a very distinct large nucleus. By degrees the outline of the latter becomes fainter; at last the nucleus vanishes after two flatly-spherical accumulations of granular matter have made their appearance between its periphery and the inner wall of the cell (Pl. LIII, fig. 9). After the disappearance of the membrane of the primary nucleus the above accumulations of mucilage immediately assume an ellipsoidal shape, and appear as two secondary nuclei (Pl. LIII, fig. 11). Sometimes the spore-mother-cell now divides by a transverse septum, after the constriction of its contents at the equator (Pl. LIII, figs. 10, 12), and each of the two halves—after the dissolution of their ellipsoidal nucleus, and the appearance of two globular daughter-nuclei—is divided into two daughter-cells having the form of quadrants of a sphere (Pl. LIII, figs. 15—17). Sometimes, however, the two secondary nuclei of the mother-cell are dissolved before the commencement of the division of the cell; four tertiary spherical nuclei appear (Pl. LIII, figs. 13, 14), and the cell divides at once into four daughter-cells. This latter case is by far the most uncommon one. At their first appearance the four nuclei usually lie in one plane, and the four daughter-cells of the mother-cell (the special-mother-cells) retain, as in the first case, the form of quadrants of a sphere. It is only very rarely that the special-mother-cells are arranged in the angles of a tetrahedron. The septa by which the special-mother-cells are separated are of a gelatinous nature. They swell up easily and quickly in water. If their contents are made to contract by the application of diluted acids, the cell walls swell up into a mass similar to that into which the contents contract.

The special-mother-cells of the small spores separate very shortly after their formation. When separate they retain their three-edged (rarely six-edged) form. Now, for the first time—by analogy to the similar phenomenon in Equisetum—there is produced in each special-mother-cell a daughter-cell, whose form exactly corresponds with that of the special-mother-cell. The daughter-cell becomes

clothed with an episporium (Pl. LIII, fig. 18), of the nature described at the commencement of this chapter, and becomes free by the dissolution of the special-mother-cell, some time before the rupture of the walls of the sporangium permits the escape of the spores, whose outward appearance, when ripe, exhibits no farther change. The special-mother-cells of the large spores, which have always a tetrahedral arrangement, remain for a longer time united in fours—even until after the formation of the exosporium.*

Alexander Braun's observations have shown that amongst the species of Isoetes, those at least of the old world, *Isoetes lacustris* is the only one which has only one furrow on the underside of the stem. All others, the South-West European and the North African species, have three, in exceptional cases, four, deep indentations of the under surface of the principal axis. The new roots break forth from the base of the deep furrow; in the species which inhabit dry localities these roots are far more numerous than in *Isoetes lacustris*. Even in the three-furrowed species the form and structure of the wood always corresponds exactly with the number and position of the furrows of the bark. The lower portion of the wood is three-armed: it consists of three laterally-flattened arched masses of wood, meeting at angles of 120°, and formed out of the closely crowded rudiments of the vascular bundles of the roots, and of the tissue between these vascular bundles, part of which tissue is changed into spiral cells, and part remains thin-walled. Where the number of roots is much greater than in *Isoetes lacustris*, as is the case especially with *I. Hystrix* and *I. Durieui*, the development of the lower part of the wood also is unequal. Each of the three arms of the lower half of the wood meets one of the deep cortical furrows (Pl. LIII, fig. 20). The newly formed roots originate the lower arched margin of the plate of wood; they bend in an arcuate manner, and breaking through the side-walls of the furrow, make their appearance at the deepest part of the latter. Many cycles of roots are developed in each vegative period; I have seen as many as eight in old strong plants of *Isoetes Hystrix*. In the greater number of the

* Wahlenberg, 'Flora Lapponica,' Pl. xxvi, fig. 1, K.

roots of such plants it is manifest that the uppermost roots of the individual rows are the youngest, a fact which is not so easily seen in *Isoetes lacustris*. In the three-furrowed Isoetes also the vascular bundles of the roots are excentrical; they are pushed towards that side of the root which is turned towards the cortical furrow in which the root breaks forth. The yearly renewal of the bark by the development of the mantle of cambium which also surrounds the lower three-armed portion of the wood, causes the removal of the older roots in a lateral direction away from the indentation of the stem in which they first appeared, and pushes them downwards and outwards. In the three-furrowed species however this change of position is less remarkable than in *Isoetes lacustris*.

In the three-furrowed species the stem occasionally exhibits a fourfold division; this appears to happen most frequently in *Isoetes tenuissima*, I found it to occur in two specimens out of seven. In stems of this sort the lower portion of the woody mass is four-armed.

The terminal bud of most of the three-furrowed Isoetes is far more deeply buried than even in *Isoetes lacustris* (Pl. LIII, fig. 21). This partly arises from the proportionably greater number of the leaves, and the consequently more rapid increase of the cortical tissue. One essential cause of the phenomenon is, however, the circumstance that the cambium-layer—which clothes the cylindrical portion of the woody mass, and which becoming prominent at three places, as in *Isoetes lacustris*, reaches to the outermost ends of the upwardly-curved arms of the lower portion of the wood—has far greater vigour, on account of the much more considerable radius of the lower portion of the woody mass. The activity of the numerous layers of cambial cells, which are almost convex above, must necessarily increase the mass of the bark more rapidly than is the case in *Isoetes lacustris*.

The leaves of the three-furrowed species, the multiplication of whose cells usually agrees with that of *Isoetes lacustris*, exhibit a far greater variety in their morphology and anatomy. The stipule-formation mentioned in a previous part of this chapter is an example of this. The most

remarkable phenomenon, however, is that exhibited by *Isoetes Hystrix*, and *Duricui*, in the lignification of the masses of cellular tissue of the bases of their leaves,* which varies in the different varieties of these species. The cells remain in the closest connexion, and are thickened in a porous manner by the superposition of dark-brown layers upon the inner walls, so that, as in *Niphobolus chinensis*, a stony, closed bark is formed round the stem. By the development of new leaves the lignified portions of the bases of the leaves are pushed more and more outwards and—after the death of the herbaceous parts of the leaves—form a close spiny covering to the stem which can hardly be cut with the sharpest knife, and is a sad hindrance in the examination of these parts.

In the three-furrowed species of Isoetes, the end of the stem, which occupies the base of the deep and steep depression of the top of the stem, is a wart of cellular tissue of a much flatter form than in *Isoetes lacustris*. It grows like that of *I. lacustris*, by continually repeated division of the single apical cell. The nature of the cell-multiplication is, however, essentially different. The septa, an endless series of which appear in the apical cell, are turned in three different directions. The apical cell has the form of a three-sided pyramid, with the top turned downwards; the cells of the second degree are produced by the formation of septa successively parallel to each one of the lateral surfaces (Pl. LIII, fig. 22). The cells of the second degree form a spiral, winding round the middle point of the primary cell, which spiral, as far as observations have hitherto gone, is always a right-handed one, and becomes a snail-shell-spiral, in consequence of the fact, that the cells of the second degree from the time of their formation grow by expansion and multiplication in all three directions.

As far as observations have hitherto gone, all the septa formed in the apical cell and turned in one of the three directions, are at right angles to a plane passing through that indentation of the stem which is nearest to them. Consequently, in one of the most essential

* A. Braun, l. c., pp. 35, 36.

features, the mode of growth of the terminal bud of the three-furrowed species of Isoetes agrees with that of *Isoetes lacustris*: the septa which appear in the apical cell are turned towards the furrows of the stem.

Isoetes lacustris—as is well known*—exhibits occasionally, but rarely, a three-furrowed stem. Transverse sections of the stems of plants of this kind† exactly resemble those of *Isoetes setacea*. The lower part of the woody mass has three short arms (Pl. XLVIII, figs. 6, 7). The mode of multiplication of the apical cell of the terminal bud is exactly the same (Pl. XLVIII, fig. 8).

Like the Selaginellæ amongst the Lycopods, Isoetes, in its mode of reproduction, resembles—more indeed than any other cryptogam—that group of phænogams which comes nearest to the cryptogams, viz., the Coniferæ. The prothallium, which consists of cells devoid of chlorophyll, occupies a space not much greater than the macrospore itself. It originates by free cell-formation in the interior of the spore-cell. In both respects it comports itself in a manner precisely similar to that of the albuminous body of the Coniferæ. The archegonia of Isoetes in the most essential features of their development and structure exactly resemble the corpuscula of the Coniferæ.

Amongst the dicœcious cryptogams—the cryptogams with spores of two different sizes, of which the larger produce the germs of the second, spore-bearing generation, and the smaller produce the spermatozoa by which the germs are impregnated—Isoetes exhibits more clearly than any other the necessity for the operation of both kinds of spores in the process of reproduction. In Pilularia and Marsilea the reproductive cells are surrounded by an abundance of mucilage, which hinders the examination of the spermatozoa, a state of things which occurs in many of the lower plants and animals of the most different kinds. In Salvinia observation is impeded by the firm adhesion of the small spores, and by the difference in the time of development of the microspores and macrospores when sown contemporaneously. In Isoetes, on the other hand, the

* A. Braun, 'Flora,' 1847, p. 34.

† Amongst more than 100 specimens I found only one of this kind.

mode of appearance, and the abundance, of both kinds of reproductive cells, are favorable to the observation of the origin of spermatozoa in the smaller archegonial prothallia, and not less so to the observation of the separate development of the microspores and macrospores.

The germination of Isoetes, like that of the Ophioglosseæ, is distinguished from that of the vascular cryptogams which have green prothallia in one essential point. In these the lateral cell of the limited primary axis of the embryo, from whose multiplication the (secondary) principal axis proceeds, lies in the apical region of the former. The leaf-bearing principal axis developes the first leaf on the side which is turned away from the apex of the primary axis and towards the exit of the archegonium. The first leaf lies *above* the principal bud, between it and the mouth of the archegonium, as is the case with the Ferns and the Rhizocarpeæ. In Isoetes, on the other hand, the bud of unlimited growth lies near the first adventitious root, close under the canal of the archegonium, and the first leaf lies *under* that bud. Judging from the position of the first root on the germ-plant, Selaginella would exhibit a similar state of affairs, were it not for the fact, that here the secondary principal axis of the plant, instead of producing a leaf close above its point of origin, divides into two branches, having previously grown considerably in length, and having produced a pair of opposite leaves.

In its vegetative development as well as in its fructification and germination, Isoetes exhibits a remarkable agreement with the Lycopods, in the fact that the wood-forming tissue has no parenchymatous pith in the centre, but occupies the whole of the longitudinal axis in the form of a homogeneous woody body. Nägeli's investigations* have shown that in Lycopodium a circle of vascular bundles is visible at first, but that after the differentiation of the circularly-arranged longitudinal strings of a delicate cambium, the whole of the axile tissue of the stem enclosed by the latter enters into the formation of the wood, and is afterwards changed from parenchymatal into prosenchymatal cells of various kinds. Thus in nearly allied plants,

* 'Zeitschrift für Botanik,' H. 3 and 4, p. 140.

which exhibit a considerable supplementary longitudinal development of the internodes, there is found the most decided tendency to form an axile woody body, similar to that whose production in Isoetes might—by the omission to notice the analogous phenomena in the stem of Lycopodium—be attempted to be brought into causal connexion with the complete suppression of an intercalary multiplication of the joints of the stem.

As far as our knowledge extends, Isoetes alone of all the vascular cryptogams possesses a cambium layer, which is renewed yearly, and a stem which grows in length both at the upper and lower ends; peculiarities of which the one is rendered necessary by the existence of the other. By the organization of its stem, especially that of the downward-growing portion of the wood, Isoetes approaches nearer to Dicotyledons,—such as Cyclamen and Beta,—which have undeveloped stem-joints and a stem which does not die from below, than to the few Monocotyledons with diametrically-increasing stems, such as Dracæna, Cordyline, and Tamus. The mode of arrangement of the roots which spring from the lower portion of the wood of Isoetes answers to that of the adventitious roots which break forth in vertical rows from the main root of dicotyledons, a phenomenon which Schimper and Sachs* have stated and proved to be of universal occurrence. Some of the commonest plants in cultivation, such as turnips and radishes, exhibit such a manifest regularity in the position and mode of succession of the adventitious roots, that more certain general results may in all probability be attained.

* 'Sitzungsber. Wiener Akad.,' B. xxvi (1858), p. 331.

CHAPTER XIV.

SELAGINELLA.

IN the species of Selaginella whose leaves have the $2\frac{1}{2}$ arrangement and stand in pairs opposite to one another in four longitudinal rows, the form of the growing end of the stem is that of a cone much flattened laterally. It projects far beyond the place of origin of the youngest pairs of leaves (Pl. LIV, figs. 3, 5, 7^a). The multiplication of the cells of the end of the stem goes on in the young shoot of *S. hortensis*, Metten. (*denticulata* hortul.) until the commencement of the formation of the third pair of leaves, and in *S. Galeottii* until that of the sixth pair. The multiplication is first produced by continual division of a single cell occupying the apex of the blunt cone, by means of septa inclined alternately to the right and to the left, always towards one of the small sides of the terminal bud. The form of this cell is that of a segment of an ellipsoid (Pl. LIV, fig. 8; Pl. LVI, figs. 1, 3). The formation of the above septa, like all the divisions of the cells of the end of the stem, is preceded by the disappearance of the primary nucleus of the cell,* the formation of two new smaller nuclei, and the appearance of a dark line between the two newly-formed nuclei (Pl. LIV, fig. 9). This line is easily obliterated, even by the continued action of pure water; its direction indicates that of the future septum. It is the side-view of the surface of contact of the two halves of the contents of the mother-cell.

Contemporaneously with the commencement of a new

* This primary nucleus is a globular vesicle floating freely in the fluid contents of the cell which are rendered turbid by numerous granules.

division in the apical cell, the second youngest cell of the stem which adjoins the apical cell divides into two halves by a longitudinal septum cutting the narrow side of the terminal bud, and inclined towards one of the wide sides of the end of the stem (Pl. LVI, figs. 1^b, 1^c). Each of the two halves is divided by a longitudinal septum which is concave towards the septum last formed, and cuts the boundary wall of the adjoining cell, which latter cell was produced by the multiplication of the next younger cell of the second degree. Of the two cells into which each half is thus divided one is turned towards the narrow, and the other towards the wide side of the stem. The former is a four-sided prism, the latter a three-sided one with curved lateral surfaces. The four-sided daughter-cell then divides, by a septum parallel to the longitudinal axis of the stem, into an inner and an outer cell. Frequently in *Selaginella Galeottii*, less often in other species, this latter cell-duplication is preceded by the production of a septum which cuts the upper and the free outer wall of the cell of the third degree at a very acute angle (Pl. LVI, fig. 3). This mode of cell-multiplication differs from what takes place in *Selaginella denticulata, helvetica, viticulosa, Martensi*, and others, where the more ordinary cell-succession occurs, and the result of the difference is, that a half-girdle of wedge-shaped cells is interpolated between each two of the groups of cells produced by the multiplication of a cell of the second degree. In this case the division into an inner and an outer cell by a septum parallel to the axis of the stem, takes place only in the larger, lower half of the four-sided cell of the third degree.

The three-sided cell of the third degree of the stem of *Selaginella hortensis, helvetica*, &c. is divided into two unequal parts by the formation of a longitudinal septum which is attached in a radial direction to the free outer surface of the cell, very near to the original side-wall of the cell of the second degree. The cells produced by the multiplication of the cell of the second degree are now all divided transversely by membranes which are parallel to the former boundary wall between the cell of the second degree and the apical cell (Pl. LIV, figs. 8, 9). This latter division usually occurs somewhat later in the inner cells than in

the outer cells. In *Selaginella Galeottii* the like divisions are produced—by longitudinal septa cutting the free outer surface of the cells—in both parts of the cell of the third degree adjoining the periphery of the terminal bud, *i. e.* in the upper wedge-shaped five-surfaced moiety, as well as in the lower which has six surfaces. Division by a horizontal transverse septum however only takes place in the inner cell. By this means the difference in the mode of cell-multiplication from that which occurs in *Selaginella hortensis* is removed (Pl. LVI, fig. 3).*

When the end of the stem is about to become forked there occur—in addition to the divisions of the apical cell by septa turned towards the narrow sides of the stem—divisions by septa inclined alternately towards the wide sides of the stem. The top surface of the terminal cell assumes, in consequence, the form of a parallelogram. The divisions of the apical cell in the four different directions follow one another in a left-handed spiral, as far at least as observations go. This second form of the divisions of the apical cell commences at a very early period in *Selaginella hortensis*—as early as the commencement of the formation of the fourth pair of leaves of a segment of a shoot (Pl. LIV, figs. 11, 12); in *Selaginella Galeottii* and *Martensi* they occur much later (Pl. LVI, fig. 4). In *Selaginella hortensis* the forking of the stem commences at a very early period. A transverse section through the end of the stem immediately underneath the apex, exhibits four axile cells, in which no one of the three directions of space preponderates. These cells are surrounded by a simple wreath of twelve cells somewhat stretched in a radial direction. Each two of them form one of the small sides, each four of them one of the wide sides of the terminal buds. The laterally compressed form of the stem is visible close under the apex of its growing end (Pl. LIV, fig. 7^b).

At first the portion of the axis above the youngest leaf increases considerably in thickness. The number of the

* My former notice of the succession of the divisions was ('Vergl. Unters.' p. 112), that the division of each of the halves into an inner and an outer cell followed immediately after the first division of the cell of the second degree. Repeated investigations have proved to me that the former division is preceded by a division produced by an almost radial longitudinal septum.

cells of its diameter and circumference is increased by repeated division of the two outermost cellular layers of its lower part, by means of radial septa, and of septa parallel to the longitudinal axis of the stem. Near the place of origin of the youngest leaf the longitudinal growth of the end of the stem of *Selaginella denticulata* experiences a remarkable acceleration, by the division of the cells of its outer surface by means of horizontal transverse septa (Pl. LIV, fig. 8).

The formation of the two youngest leaves commences at a distance of from eight to ten cells—reckoning downwards—from the apical cell of the terminal bud. Two horizontal opposite rows of cells, each of which occupies a fourth part of the circumference of the stem, become arched outwards, and divide contemporaneously by septa inclined downwards (Pl. LV, fig. 21). In the outer three-sided prismatic ones of the newly-formed cells, division then ensues by septa inclined in opposite directions (Pl. LV, figs. 22, 23). The young leaf, viewed from above, now appears as a narrow seam surrounding a fourth part of the circumference of the stem (Pl. LIV, fig. 7^b). It grows rapidly in length by continual division of the cells of its fore-edge by means of septa inclined alternately towards the upper or the under surface of the leaf (Pl. LV, fig. 23; Pl. LVI, fig. 12). This multiplication of the cells is far more active in the middle of the fore-edge than at its sides. The form of the leaf would sooner become pointed were it not for the fact, that the two middle cells of the fore-edge frequently divide by longitudinal septa perpendicular to the surfaces of the leaf and slightly diverging from its longitudinal axis. In the young state of the leaf one such division almost always occurs after each two divisions by septa inclined to the surfaces of the leaf. Similar divisions occur from time to time in the outer of the cellular groups near the middle of the fore-edge of the leaf (Pl. LV, figs. 24, 25; Pl. LVI, figs. 5, 6). By this means the originally parallel arrangement of the cells of the leaf becomes radiating and fan-shaped. By the repeated division of all the marginal cells of the leaf its base also becomes considerably widened. The newly-formed basal cells do not amalgamate with the

neighbouring cells of the circumference of the stem, but are developed independently, and form—when the leaf is perfected—the basal appendages which are especially employed in the determination of the species. In the greater part of its area the leaf of *Selaginella Martensi* and *S. Galeottii* continues as a double layer of cells; only the cells of a wide longitudinal strip adjoining the median line on both sides divide repeatedly by septa parallel to the surfaces of the leaf, alternating from time to time with septa perpendicular to the surface. Both divisions occur oftener in the inner than in the outer cells of the longitudinal ribs which are thus formed, and which project on the underside of the leaf. The string of narrower cells which thus originates in the longitudinal axis of the mid-rib is afterwards transformed into a vascular bundle (Pl. LVI, fig. 11).

Contemporaneously with the commencement of the thickening of the mid-rib, a longitudinal expansion of the apex of the leaf begins, an expansion, that is, of the middle cells of the fore-edge, which by their more frequent divisions have in the mean time shot ahead of the neighbouring cells. The walls of these become thickened; in the place of the faintly-green mucilage which has hitherto filled the cells, sharply defined chlorophyll granules make their appearance in the fluid contents, which have become transparent. After the commencement of these processes a multiplication of the superficial cells of the base of the leaf ensues, by the division of such cells, once at least, by longitudinal and transverse septa perpendicular to the surfaces of the leaf. The cells of the under-side divide once oftener than those of the upper-side, such division being produced by septa at right angles to the longitudinal axis of the leaf. In the perfect leaf the cells of the under-side are always about one half shorter than those of the upper-side, which latter, instead, divide once oftener by longitudinal septa, so that they are only half as wide as those of the under-side (Pl. LVII, fig. 8).

The double row of cells of the upper surface of the leaf, which lies in the angle between the leaf and the stem, and immediately adjoins the circumference of the stem takes no part in these divisions. These cells remain consider-

ably larger than their neighbours (Pl. LVI, fig. 12). Their free wall becomes arched upwards; the cell farthest from the stem then divides by a septum inclined away from the longitudinal axis of the stem. The double layer of cells which rises in the form of a wall thus receives an addition of a row of top cells. These continue to divide by septa inclined alternately in two directions; the result is that a flat membranous cellular body is produced from the upper side of the base of the leaf (Pl. LV, figs. 26, 27; Pl. LVI, figs. 11, 12). This body was first observed by R. Müller,* and is a kind of ligulate formation, most nearly resembling, on the one hand the coronet of the perigone of the Narcissi and the ligule of the grasses, and on the other hand the scale in Isoetes. I shall merely call it a stipule.

The cells of the stipule which are raised above the surface of the leaf very soon divide by longitudinal septa perpendicular to the upper and under side of the stipule (Pl. LVI, fig. 9), and afterwards also by transverse septa at right angles to the surfaces of the organ. This multiplication continues in the base of the stipule for some time after the multiplication of the apical cells has ceased (Pl. LVI, fig. 11).

At a later period the number of the cells of the organ in the direction of the thickness, is increased by the division of the cells of its lower portion parallel to the surface (Pl. LV, fig. 27; Pl. LVI, figs. 11, 12). The double row of basal cells sunk in the substance of the leaf does not increase in number, but the cells increase considerably in size. As the longitudinal growth of the stipule draws to a close, its apical cells, in *Selaginella Galeottii* and others, divide only by transverse septa perpendicular to the surface. The upper end of the stipule becomes a simple cellular layer. The margin, in all species, exhibits a delicate fringe, caused by the papillate outgrowth of individual cells (Pl. LV, fig. 28). The cells of the stipule contain granular mucilage which is colourless or grey or—under transmitted light—of a reddish colour. They never contain chlorophyll. Like the stipules of the greater number of those phænogams in which stipules occur, the development of the stipule of

* 'Bot. Zeit.,' 1846.

Selaginella terminates long before that of the leaf to which it belongs. It is only to be found in full vitality amongst the closely crowded leaves of the bud; in the axils of those leaves between which the last longitudinal expansion of the stem began it is always shrivelled and inconspicuous. Spring, who has written a monograph of the family, has not himself seen the organ.

That region of the young leaf which, by repeated division parallel to the surface of the cells of the underside, becomes transformed into the mid-rib, corresponds exactly in breadth with the place of attachment of the leaf. This breadth in the youngest state of the leaf, and up to the time when the formation of the mid-rib begins, is equal to one fourth part of the circumference of the stem. It is afterwards much less, inasmuch as after the commencement of the formation of the leaf the number of the cells of the circumference of the stem continues to increase. Each of the transverse rows of cells of the circumference of the stem—by whose multiplication a leaf is produced belonging to one of the four longitudinal rows in which the leaves of the greater number of the species of Selaginella are arranged—stands immediately above the place of insertion of the next lower leaf (Pl. LV, figs. 11, 12). The circumference of the stem becomes thickened as in the Equisetaceæ by the growth in thickness of the bases of the leaves, which originate close above each other, and by the often repeated division, parallel to the longitudinal axis of the leaf, of the cells of the base of its under-side. Its periphery appears to be formed of a number of cellular layers produced by the multiplication of the cells of the young rudiment of the leaf (Pl. LV, fig. 11). The axile cells of the stem which correspond with the naked end of the bud—which naked end projects above the rudiment of the youngest leaf—enter for the most part into the formation of the vascular bundles and the parenchyma between them.

When the leaf is almost fully formed every other one of its marginal cells expands laterally into a blunt papilla, whih becomes rapidly elongated, often to a very consider-able extent, as for instance at the base of the upper leaves*

* The "Intermediären Blätter" of Spring.

of *Selaginella Martensi*. The papilla assumes a conical form. The sharp apex of these unicellular hairs, which represent the teeth of the margin of the leaf, are soon entirely filled by rapid thickening of the walls. The conical mass of cellulose often bears a deceptive resemblance to a small cell, owing to the seam of light which its edges exhibit when seen with transmitted light (Pl. LVI, fig. 7). The two rows of cells of the upper side of the leaf which immediately adjoin the marginal cells, exhibit in many species definite appendages of the outer wall. For instance, *S. Galeottii* has two longitudinal rows of bluntish warts, similar to those on the outer side of the hairs of many Borragineæ (Pl. LVI, fig. 7).

Numerous chlorophyll-granules are formed in the narrow cells of the upper surface of the leaf In *S. Galeottii* and *Martensi* they have a distinctly vesicular appearance, and contain some very small starch granules. In the square cells of the underside of the leaf the green mucilage coagulates into a single large spherical ball, as is the case in Anthoceros (Pl. LVI, fig. 8). At the places where the cells of the under-surface of the leaf adjoin those of the upper, a connected net-work of air-cavities is produced by the parting asunder of the edges of contact of the cells of the under side from the closely connected cells of the upper side of the leaf. The place of contact of each cell of the under surface of the leaf with the cells of the upper surface is surrounded by an air-cavity which is usually six-sided. Towards the outside the cells of the under-side of the leaf are in close connexion.

The Lycopodiaceæ in general, and especially the species of Selaginella, whose stems are elliptical in a transverse section, afford some of the most marked instances of true forking of the apex of the stem, which are to be found in the whole of the vegetable kingdom. In all species of Selaginella, whose leaves have the $2\frac{1}{2}$ arrangement, a forking of the stem occurs, almost without exception,* after each four circuits of leaves; and the same thing occurs also in those species whose shoots are apparently quite simple and undivided for a considerable dis-

* The only exceptions I know are seen now and then in *S. helvetica*.

tance. In *S. viticulosa* and *cordifolia* also, a rudimentary few-leaved axis may be found on the lower part of the upright shoots of the second order which spring from the creeping stem: it is situated between each fourth upper and under leaf, and is hidden alternately in the right and left edge of the stem. If the upright shoot is broken off, these buds, which otherwise remain dormant, are developed into upright shoots.

When the end of the stem is about to fork, the apical cell divides by a vertical septum, instead of by a septum inclined in the opposite direction to the septum last formed. In both the newly-formed cells this division is usually repeated once or several times (Pl. LVI, figs. 7^c, 9, 10), whilst the number of cells of the next lower portion of the stem in the direction of the largest transverse measurement of the two edged stem is correspondingly increased by repeated longitudinal divisions. In the two outermost cells of the row of cells thus formed which crowns the apex of the end of the stem, a division ensues by a septum strongly diverging from the axis of the shoot. The wedge-shaped one of the two newly formed cells is immediately divided by a septum inclined in the opposite direction. Thus the development of two new shoots, in the manner pointed out in a previous part of this chapter, is brought about (Pl. LV, fig. 10). This happens normally immediately after the commencement of the formation of the last leaf of the forking shoot, even before these leaves are clearly visible above the circumference of the stem.

Many species, for instance *S. Martensi*, *Galeottii*, and *viticulosa*, exhibit a feature which is found in the Ancuræ. Either the right or the left fork of the stem, alternately, develops itself more vigorously than the other, and soon pushes the latter entirely on one side. These species seem to be furnished with a principal shoot, which sends forth adventitious shoots to the right and to the left. On the other hand, in *S. hortensis*, *helvetica*, *&c.*, the forks of the terminal bud are developed quite equally in length and thickness. The forking end of the stem here assumes at first the shape of a spatula (Pl. LIV, figs. 7^a, 10); in consequence of the rapid development of the forked shoots con-

stituting the edges of the spatula-like flat cellular mass, the fore-edge of the latter soon appears deeply indented (Pl. LIV, figs. 3, 5). In one respect, however, even here there is a preponderance of the development of one branch of the fork; the right or left fork, alternately, forms a primary leaf* before its sister-shoot, even before the division of the end of the stem is manifest. This leaf, therefore, appears to be situated on the middle of the underside of the forking end of the stem (Pl. LIV, figs. 5). By the subsequent growth of the shoot it is pushed more on one side.

Each shoot of Selaginella is traversed in its upper portion by two thin cylindrical woody bundles, whose position corresponds with the foci of the ellipse represented by the transverse section of the stem. Towards the base of the shoot, near the points of junction with the other branch of the fork, the two bundles unite to form one (Pl. LIV, fig. 3). The differentiation of these vascular bundles from the surrounding tissue of the stem first takes place in *Selaginella Galeottii* underneath the second youngest pair of leaves. The cells destined to form the vascular bundle lag behind the neighbouring cells in transverse division, and divide repeatedly by longitudinal septa radial to the axis of the stem and parallel to it. This takes place even later in *S. hortensis*, some-time after the commencement of the forking of the naked end of the shoot in question. In this species the remarkably regular furcation of the vascular bundle of each shoot † is manifestly in connexion with the succession of the forkings of the stem.

The cells immediately adjoining the vascular bundles take no part in the remarkable longitudinal expansion of the cells of the stem by which the leaves are removed far from one another, and the first clear distinction between stem and leaves is produced. The stretching of the neighbouring cells of the bark and of the pith, as well as of the vascular bundle itself, soon removes those cells from one another, so that they have the appearance of proportionably thin threads, which unite the vascular bundle—which is

* Feuille primaire, Spring.

† See 'Kaulfuss Wesen der Farrnkräuter,' p. 25.

placed in the middle of a hollow cylindrical air-cavity—with the remaining tissue of the stem (Pl. LVII, fig. 11). These cells afterwards divide by a transverse septum, once at least in those species in which the air-cavities have a proportionably narrow diameter, and several times in those species where the air-cavities attain a considerable development, as in *Selaginella helvetica*.

A string of cells passing from the vascular bundles of the stem through the thickened longitudinal axis of each of the neighbouring leaves, becomes transformed into a vascular bundle whose nature and structure resembles in its essential features those of the stem. The formation of the vascular bundles always commences earlier in the stem than in the leaves; it progresses from the former towards the latter (Pl. LVI, fig. 11).

Adventitious roots spring from the forks of the stem; in *S. denticulata* and *helvetica* they spring from each fork, after the commencement of the final longitudinal expansion of the stem. In *S. Martensi* and *Galeottii*, and still more so in *S. viticulosa* the upper ramifications of the upright shoots, which have a tendency to produce fruit, are apt to be devoid of roots. The root is always situated in the angle of the *primary leaf*, which in the bud apparently occupies the middle of the forking end of the stem. It originates on the outer side of the transverse junction which in the fork of the stem unites the two vascular bundles (Pl. LIV, fig. 3). The mode of cell-multiplication in the growing tip of the root exactly resembles that in the Equisetaceæ and Polypodiaceæ; the examination of it is much more difficult than in the latter plants on account of the smallness of the cells. The roots of the Selaginellæ, like those of the Lycopodiaceæ in general, are usually several times branched; they exhibit the most regular furcations in two directions diverging from one another at about 90°. The first fork of a root is usually parallel to the surfaces of the leaf in whose axil it has originated, and the second at right angles to those surfaces.* The outer side of the root-cap is often clothed with long papillæ, which, as the

* The relation is very manifest in the roots of *S. Galeottii*, and *Martensi* which ramify frequently high above the ground.

organ becomes further developed, are thrown off with the cells which bear them. The adventitious roots of the larger species fork frequently even long before they reach the ground. Those of *S. hortensis* usually ramify for the first time after they have penetrated into the ground. The foundation for the first ramification is however here also laid at an earlier period. The aerial roots as soon as they have reached a certain stage of development exhibit a spherical enlargement of the end.* This thickening of the tip of the root is formed by the commencement of furcation: the lenticular cell of the first degree of the root has divided by a longitudinal septum into halves, each of which commences an independent multiplication in a direction away from the other. The two rudimentary branches thus formed, surrounded by the outer cellular layers of the root, which were formed before the commencement of the forking, constitute the almost spherical mass of the end of the root.

It is a known fact that the smallest fragment of the stem of Selaginella when properly treated—that is, kept moist and warm upon loose earth—will produce a new plant. This depends upon the production of adventitious roots in definite positions: in the angles formed by the vascular bundles which branch off into the leaves with the vascular bundles of the stem. The adventitious shoot breaks through the cortical layer of the stem and is developed into a new plant by a succession of shoots, in the same manner as an embryo is produced by impregnation of an archeognium, after an adventitious root has grown out close to its place of origin (Pl. LVI, fig. 10).

Fruit is formed in Selaginella only on particular shoots differing greatly in their habit from the vegetative shoots. The branch destined to develope sporangia is, like the vegetative branches, a fork of the naked end of the shoot of the preceding order. It is distinguished from the vegetative shoots even in its earliest condition by a far less rapid increase in length, so that, even in *Selaginella denticulata*, it is soon pushed to the side of the vegetative shoot—whose direction is the same as that of the shoot of the preceding order—and might be taken for an immediate prolongation

* Kaulfuss, Wesen der Farrnkräuter,' p. 64.

of it (Pl. LIV, fig. 3). The mode of cell-multiplication in the growing end of the fruit-branch resembles that of the terminal bud of vegetative shoots (Pl. LV, fig. 29), with this difference only, that the growth in thickness is uniform on all sides. The transverse section of the fruit-branch is circular not elliptical.

A sporangium is produced in the axil of each of the equal-sized leaves of the fruit-branch—which leaves have the $2\frac{1}{2}$ arrangement—with the exception of the two or three first, lowest leaves. The first rudiment of the sporangium is produced by the division, by means of a septum almost perpendicular to the outer surface of the terminal bud, of one of the cells of the circumference of the stem close above the middle point of the place of attachment of the youngest leaf. This is followed by the production of septa at right angles to that surface in the sporangial cells of the second degree, and of septa parallel to it in the sporangial cells of the third degree (Pl. LV, figs. 1, 2). As soon as the organ has the appearance of a hemispherical lateral outgrowth of the end of the stem, a central cell may be seen, surrounded by a simple layer of cells, and borne upon a short stalk consisting of a few cells. In *Selaginella helvetica* this central cell is much larger than its neighbours (Pl. LIV, fig. 2). In *S. hortensis* the cells which bear it divide for the first time at a late period by septa parallel to the longitudinal axis of the sporangium. In this species the cell in question appears as the uppermost of a string of cells traversing the axis of the rudimentary sporangium (Pl. LV, fig. 3).

The enveloping cells divide repeatedly by septa perpendicular to the outer surface of the young fruit, alternating twice with septa parallel to that surface. The wall of the sporangium soon becomes a double cellular layer and ultimately a triple one (Pl. LV, figs. 4—6). The cells of the stalk also divide repeatedly by septa parallel to the longitudinal axis and perpendicular to it; the stalk of the sporangium rapidly becomes both longer and thicker. In the mean time the central cell also multiplies, although more slowly, by repeated bipartitions in all three directions (Pl. LX, figs. 4, 5). In a mass of fruit of Selaginella

even the fifth-youngest sporangia have the appearance of a central group of larger cells (the mother-cells of the spores) with grumous contents and large nuclei, surrounded immediately by a layer of delicate, mucilaginous, radially-extended cells, similar to those which surround the string of mother-cells of the anthers of phænogams. This layer is followed by a layer of tabular, thick-walled, chlorophyll-bearing cells, which supports the epidermis of the sporangium: these chlorophyll-bearing cells are radially-extended prismatic cells with watery fluid contents; in the young fruit they are four times smaller than the chlorophyll-bearing cells immediately below: when the fruit is almost ripe they are—in consequence of repeated divisions—almost sixteen times smaller than the same cells (Pl. LV, figs. 5, 6, 16).

This multiplication of the cells of the young sporangium takes place mainly in the direction of the breadth; the organ assumes the form of a laterally-flattened ellipsoid, which in the macrosporangia passes by degrees into the shape of a kidney, and in the microsporangia becomes more elongated. The leaf in whose axil the sporangium originates, does not begin to develop its stipule until a later period, when the young fruit has attained a considerable size, and the central group of spore-mother-cells has almost completed its full number (Pl. LIV, figs. 3, 4).

The mode of development of the sporangium shows most distinctly that the latter cannot be considered as a transformed portion of a leaf, unless * the group of cells which is formed close above the place of insertion of the stipule, above the apex of the angle between the latter and the stem, is considered as belonging to the leaf and not to the stem. This supposition is only difficult to reconcile with the observed youngest conditions of the leaf and sporangium. The young rudiment of the fruit, when consisting of only very few cells, is generally situated on the outer surface of the end of the stem (which outer surface is turned towards the leaf,) even in those species, like *Selaginella helvetica* and *spinulosa*, whose sporangia, when only

* See von Mohl 'Vermischte Schriften,' p. 106.

slightly developed, are pushed so far upwards on the upper surface of the next lower leaf that they appear to form a portion of it (Pl. LIV, fig. 1; Pl. LVI, fig. 30). In the vascular cryptogams there are the like difficulties in obtaining a clear idea of the relation of the sporangium to the leaf, as are met with in observing the relations between the placenta and ovules of phænogams, and the carpels. The same considerations must find a place here, and on this account I would withdraw my former assent to the explanation * of the sporangium of Selaginella given by Bischoff, who described it as a metamorphosed axillary bud, and adopt von Mohl's view, the probability of the correctness of which is supported by the relation between the sporangium of Isoetes and its leaf and leaf-scale, the latter being the manifest analogue of the stipules of Selaginella.

As the sporangium becomes older the spore-mother-cells become individualised, after a moderate thickening of their walls. They then form spherical cells with turbid mucilaginous contents and a rather large nucleus. They are closely crowded together and fill the cavity of the fruit (Pl. LV, fig. 6).

Up to this point the history of the development of all sporangia is the same. Henceforth however, as in all the Rhizocarpeæ, the subsequent development exhibits essential differences, according as the sporangia are destined to become microsporangia or macrosporangia, *i. e.* to produce small or large spores. In *Selaginella hortensis* the lowest sporangium only of each mass of fruit becomes a macrosporangium; that one, namely, which is formed in the axil of the lowest one of that longitudinal row of aristate leaves which is situated vertically over the last *primary leaf* on the right or left side of the shoot of the preceding order. By the rapid and remarkable increase in size of the fruit the latter grows beyond the lateral margins of its own covering leaf, so that the two next lower ones also, which are sterile leaves belonging to other longitudinal rows of the fruit-ear, have to take part in covering the fruit.

Of the many free spherical cells of the interior of the young macrosporangium, one single cell only, not distin-

* 'Vergl. Unters.,' p. 119.

guished in any respect from the others,* becomes slightly increased in diameter, its primary nucleus becomes dissolved, and four new nuclei are formed. This cell then divides into four tetrahedral daughter-cells, the special-mother-cells of the spores, by six septa cutting one another at angles of 120° (Pl. LV, fig. 7). Almost immediately afterwards there is formed in each of the special-mother-cells a cell almost filling the latter, and having at first very delicate walls. This cell is the spore. The four spores immediately begin to become individualised by the gradual dissolution of the wall of the special-mother-cells (Pl. LV, figs. 8, 9, 10), and they assume a spherical form. The loci of the commissures of the special-mother-cells are indicated by very slightly prominent ridges (Pl. LV, figs. 11^b, 12^b). The product of the dissolution of the special-mother-cells (which cannot be seen by direct observation) appears to retain the spores for some time longer in somewhat close proximity.

Soon after the separation of the spores the formation of the outer spore-membrane commences. The inner transparent layer† is first visible (Pl. LV, fig. 11^b), and soon afterwards the outer one also, which is composed of a quantity of two different substances varying in their refractive power. Both layers take part in the composition of the long spines of the exosporium, which are united by reticulate ridges (Pl. LV, fig. 17). During their formation the three converging ridges at the top of the spore become somewhat more conspicuous; each of them now appears to be traversed by a fine longitudinal fissure. The spines appear as slight projections of the inner glassy layer (Pl. LV, fig. 13), and gradually increase in length. When quite ripe they appear considerably shorter than when half-developed. It would seem that the pressure which the rapidly-growing spores exert upon one another breaks

* In some cases I was convinced that this cell floated almost in the middle of the macrosporangium. At the time when one of the free spherical cells becomes (by division into four) the mother-cell of the spores, the free spherical cells no longer entirely fill the inner cavity of the macrosporangium; a space filled with watery fluid is found above the place at which the stalk is attached to the capsule.

† Under transmitted light this layer is at first as clear as glass, then straw-coloured, and ultimately brown.

off the points of the spines. Shortly before the spontaneous rupture of the macrosporangium the spores adhere rather firmly to its inner wall by means of their spines.

During the formation of the large spores the macrosporangium changes its form very considerably. By a vigorous local multiplication and expansion of the cells of the wall, two hemispherical protuberances of the latter are formed in the middle of the two lateral surfaces of the reniform sporangium which are turned towards the stem and the covering leaf. This occurs even long before any one of the four spores has touched the inner wall of the sporangium (Pl. LV, fig. 11[a]). The top of the organ also becomes more steeply arched. At this time the spores still float freely in the watery contents of the macrosporangium, in company with the numerous unchanged sister-cells of the one spherical cell, which, by its division, becomes the mother-cell of the spores. Four or more of those small delicate-walled cells are often found still loosely adhering to one another, a remnant of the innate connexion which in the earlier stages of development of the sporangium subsisted amongst the mother-cells. The layer of radially-extended, mucilaginous, actively-multiplying cells which clothes the inner wall of the capsule exists up to this time. It disappears with the further development of the spores, and the wall of the sporangium when almost ripe consists of only two layers of cells (Pl. XLI, fig. 16).

The development of the large spores of many other species, especially of *Selaginella Martensi*, *helvetica*, and *spinulosa*, differs from that above described, especially in the fact that the special-mother-cells last much longer than in *S. hortensis*.* The spore has therefore (even when fully developed) a somewhat sharply defined tetrahedral form (Pl. LV, fig. 13; Pl. LVII, figs. 6, 7), at least its apex exhibits three very distinct ridges, meeting at angles of 120°, and extending downwards for a considerable distance; this is the case in *S. helvetica*. The species in which this occurred are all species in which the macrosporangia and microsporangia, differing little if at all in their external form, are intermixed apparently without regularity. In *Selaginella Galeottii* even the very young large spores have a regular spherical form. In *S. Martensi* a considerable increase in

size takes place in that one of the many free spherical cells in the interior of the young capsule which is destined to become the mother-cell of the large spores (Pl. LVII, figs. 1—5). Four new spherical nuclei (Pl. LVII, fig. 3) are formed on the outside of its primary nucleus, which becomes more and more indistinct. Soon afterwards the primary nucleus disappears (Pl. LVII, figs. 4, 4^b), and six septa meeting at angles of 120° suddenly appear in the mother-cell (one between each two of the secondary nuclei), which represent four tetrahedral special-mother-cells. In each of the latter a spore is formed after a previous considerable thickening of the wall, and during the very remarkable increase in size of the special-mother-cells which follows this thickening. The brown exosporium is in this species very thick. In the perfect state three layers are distinguishable, the middle one of which is of a glassy nature. The thickened special-mother-cells are still in a good state of preservation. The lines of division between each two are here far more clearly distinguishable than in any phænogamous plant except the Malvaceæ (Pl. LVII, fig. 7). At this stage of development a slight pressure separates the special-mother-cells, each of which contains a spore (Pl. LVII, fig. 7^b). In a manifestly diseased state of *S. Martensi* I have seen the disproportionately thick exosporium composed of prismatic (or, to speak more accurately, of truncate-pyramidal) fragments; the spore had remained much smaller than usual (Pl. LVII, fig. 8).

During the formation of the outer membrane of the large spores of all the species which I have examined, the spherical nucleus usually lies close under the place at which the three prominent ridges of the exosporium unite (Pl. LVII, fig. 7).* It increases rapidly in size, and its nucleolus disappears. Afterwards numerous vesicular bodies appear within it (Pl. LV, figs. 13, 14). As the spore approaches maturity it appears to be dissolved: I was never able to find it in those spores which entirely fill the macrosporangium.†

* If the young spore lies for some time in water, the nucleus disappears.

† Mettenius appears to assume that the nucleus of the spore gradually expands until it attaches itself at all points to the inner wall of the spore-cell ('Beitr. zur Botanik,' H. i, p. 7). I have never seen anything indicative of such a process.

In the microsporangia all the free spherical cells of the interior divide at a somewhat early period into four tetrahedral special-mother-cells. The process is similar to that which takes place in the division of the mother-cells of the large spores of *Selaginella Martensi*. Four new smaller nuclei are formed outside the primary nucleus of the cell, apparently by the double bipartition of a spherical accumulation of formative matter. Between each two of them the six double walls appear which separate the individual special-mother-cells from one another. The commissure of the septa of each two special-mother-cells is often very perceptible even in the mother-cells of the small spores, notwithstanding the minuteness of the object (Pl. LVII, fig. 10^b). In each of the special-mother-cells a spore is formed, which in many species (for instance in *S. Martensi*) produces wonderfully long spines on the outside of the exosporium after the absorption of the special-mother-cells. On the other hand the outer membrane of other species, such as *S. helvetica*, appears only slightly granulated. All small spores of Selaginella exhibit at the apex three converging ridges of the outer spore-membrane. In the microsporangia of cultivated tropical species of Selaginella, malformations are not uncommon. Thus in *S. Martensi* it frequently happens that a mother-cell divides into two or three special-mother-cells only,* of which three, two only produce spores (Pl. LVII, fig. 11); or sometimes, out of a mass of special-mother-cells, two or even three become shrivelled, whilst the rest retain their vitality. In one case I saw the following singular phenomenon. In one sporangium, containing several abortive and several apparently healthy sets of mother-cells, eight oval cells occurred, more than three times as large as the largest special-mother-cells, and having a disproportionately thick, glassy, transparent wall, which exhibited manifest lamination: the cell-contents consisted of concentrated granular mucilage and a rather large nucleus (Pl. LVII, fig. 12).

The large spores only of the Selaginellæ produce prothallia. The first rudiments of the latter are formed before

* As in R. Brown's *Triposporium*.

the bursting of the macrosporangia. A circular simple cellular layer appears spread over the inner side of the primary spore-membrane, underneath the point in which the four special-mother-cells of the spores touch one another. Those cells are of the greatest height which are situated in the middle of the cellular layer underneath the point of junction of the three projecting ridges of the outer spore-membrane; they divide very soon by transverse septa. Towards the periphery the cells gradually diminish in height; the outermost have the form of a procumbent wedge (Pl. LVII, fig. 16). In many species, especially *S. hortensis* and *helvetica*, the rudiment of the prothallium when seen from above appears to have no distinct boundary, inasmuch as the outermost edge of the marginal cells formed by the convergence, at a very acute angle, of the upper and under wall of the cell, does not refract transmitted light much more powerfully than the primary wall of the spore itself. The marginal cells of the prothallium when seen from above appear open towards the outer side (Pl. LVII, fig. 17).* The prothallia of other species, for instance of *S. Martensi*, exhibit nothing of the sort (Pl. LVII, fig. 18).

I have not yet made out the first stages of development of the rudiment of the prothallium. It is uncertain whether it is formed, like the prothallium of Marsilea, by repeated bipartition of a single cell, or whether, like

* I believe that the above explanation is sufficient to explain the peculiar phenomenon. Mettenius ('Beitr. zur Botanik,' Part 1, p. 10), deduces from it a mode of development of the cells of the prothallium, which would differ very widely from all other phenomena hitherto observed in the vegetable kingdom. He believes that the prothallium originates between two lamellæ of the wall of the spore, which separate from one another; that it increases gradually in circumference whilst those lamellæ become further separated from one another, and that new cells are added to the circumference of the prothallium in a manner which—even if it is not yet fully investigated—offers no points of resemblance with the hitherto better known forms of cell-formation. I consider Mettenius's conclusions to be incorrect, especially because the small-celled portion of the prothallium from which the archegonia are produced occupies when fully developed (Pl. LVIII, figs. 1, 4), no relatively greater portion of the circumference of the spore than it does when it first becomes visible. I consider it much more probable that the empty cells figured by Mettenius in fig. 10 of the first plate of his work, should be cells, which, by the development of the large-celled inner portion of the prothallium have been pressed against the outer spore-membrane, and squeezed together so as to obliterate the cavity, than that they should be cells in a formative condition.

the endosperm of the Coniferæ — which in so many respects resembles the prothallium of Selaginella—it is formed by the attachment of originally free cells to the inner wall of the large spherical firm-walled cell (the spore or embryo-sac) in which it originated.

In the above state the large spores are discharged from the ruptured macrosporangium. In *S. hortensis* and *helvetica* their further development is preceded by a dormant condition which lasts for several months. During the latter, the walls of those cells of the prothallium which adjoin the spherical inner cavity of the spore become thickened. Thickening layers are formed on both their sides, leaving, in some cells, wide circular pits free (Pl. LVIII, figs. 1, 2). By taking longitudinal sections of these pits it is seen that the thickening of the walls is most considerable on that surface which is turned towards the interior of the spore. The contents of this large spherical cell secrete cellulose and cause a thickening not only of the septa which separate the contents from the cells which have attached themselves to the inner wall of the apex of the spore, but also of the free portion of the inner surface of the primary spore-membrane, so that the latter becomes a very compact glassy membrane $\frac{1}{1250}'''$ thick. The contents of the large cavity of the spore consist during this period of a mixture of albuminous and oily matter. These phenomena are most remarkable in *S. hortensis*, less so in *S. helvetica*. In *S. Martensi* and other tropical species the large spores germinate a few weeks after being sown, and the above thickenings of the walls are hardly perceptible (Pl. LVII, fig. 19).

When the further development of the prothallium commences, its cells divide repeatedly by longitudinal septa perpendicular to the outer surface, and by transverse septa parallel to that surface. This cell-multiplication begins in the middle point of the prothallium, proceeds from thence towards the periphery, and ceases long before it reaches the latter (Pl. LVII, fig. 6). Before the repetition of the division by transverse septa archegonia are formed.

The first archegonium appears exactly at the apex of the prothallium; those which are lower down are of later origin.

The formation of the archegonium commences by the division by means of a transverse septum of one of the cells of the upper side of the prothallium. This is followed by the division of the upper cell by a longitudinal septum, and the division of the two halves by a septum at right angles to the one last formed and perpendicular to the free outer surface. Each of the four narrow tall cells which are situated above the larger basal cell, is divided by a horizontal septum into two parts of which the under half is usually the lower in height (Pl. LVIII, fig. 1). The four apical cells of the archegonium generally arch out into short papillæ (Pl. LVIII, fig. 2). By the parting asunder at their edges of contact of the four parallel pairs of cells, a narrow passage is formed, leading to the basal cell (Pl. LVIII, figs. 1^b, 4). In the latter a spherical cell is produced almost filling the mother-cell and rich in finely granular protoplasm. All the narrow cells of the prothallium now exhibit distinct nuclei if sufficiently fine sections be taken. The outer walls of the cells of the upper side, especially those of the apical cells of the archegonia appear at this time remarkably thickened (Pl. LVIII, fig. 2).

Contemporaneously with the development of the archegonia a tissue of wider cells becomes visible spread over the under side of the small-celled portion of the prothallium (Pl. LVIII, fig. 1). The middle of this cellular mass projects into the unoccupied portion of the inner cavity; it hangs downwards from the inner wall of the primary spore-membrane for some distance beyond the first-formed portion of the prothallium. Its marginal cells repeat the form of that of the older cellular layers; they are wedge-shaped, and their under side forms a very acute angle with the inner wall of the spore. In *S. Martensi* a similar large-celled tissue fills the entire cavity of the spore-cell.

There is only one species, viz. *S. helvetica*, in which I have been able to ascertain the behaviour of the small spores after they are set free. In this case however there was no doubt. Five months after the beginning of March, at which time they were sown upon earth mixed with fine sand and kept continually moist, a large number of very

small * spherical cells were formed in almost every small spore, and nearly filled its cavity (Pl. LVII, fig. 13). By careful pressure these cellules escaped through the fissures of the ruptured spore-membranes. They contained either a finely granular protoplasm,† or a very fine, thin spermatozoon, rolled up spirally, which when free moved slowly (Pl. LVII, fig. 15).

The production of spermatozoa in the small spores terminates long before the complete formation of the prothallium. In *S. helvetica*, as has been said, it ceases five months after the sowing of the spores, whilst the first archegonia on the prothallia of large spores sown at the same time, did not appear until six weeks later. This is no doubt the reason why all experiments with the large spores yield no result—whether sown separately or mixed with the small spores—where the possibility of the subsequent access to the prothallia of small spores of the same species, is precluded.‡ The young plant or embryo is formed by the repeated bipartition of the one daughter-cell produced in the basal cell of the archegonium. It does not often happen that more than one archegonium of the same prothallium is impregnated. The abortive archegonia, especially those low down on the prothallium, often exhibit a peculiar luxuriant growth of their apical cells § (Pl. LVIII, figs. 4, 5). The first division of the mother-cell of the embryo (the germinal vesicle) takes place by a transverse septum (Pl. LVIII, fig. 3).‖

It happens occasionally but rarely that the embryo originates immediately from the lower of the two cells, and that all its daughter-cells take part in the formation of the massive portion of its first axis (Pl. LVIII, fig. 6). The

* Diameter $\frac{1}{350}'''$ or less.

† See Pl. LVII, fig. 13. I consider these cellules as not fully developed.

‡ When I sowed the large and small spores together, and covered them with a hand-glass, all the sowing failed. *Spring* was similarly unsuccessful ('Monographie de la famille des Lycopodiacées,' extraite des tomes xv et xxiv des 'Mémoires de l'Académie Royal de Belgique,' Bruxelles, 1842 et '49, p. 316, note). On the other hand when richly-fruiting specimens of the same Selaginella were brought under the hand-glass, embryos soon appeared.

§ The process is very accurately explained by Mettenius, 'Beiträge,' Part 1, p. 12.

‖ See the note to this figure in the explanation of the plates.

commencement of the formation of the first axis—which takes place by division of the terminal cell of the short pro-embryo by alternately inclined septa—is usually preceded by the division (from once to three times) of the terminal cell of the bicellular pro-embryo (embryo-bearer) by transverse septa. During this process a very considerable longitudinal expansion of the upper cells of the pro-embryo takes place, in consequence of which its lower end is pushed deep down into the tissue of wider cells, which tissue in *S. hortensis* now fills about a third part (Pl. LVIII, fig. 4), and in *S. Martensi* the whole of the cavity of the spore.

By the multiplication in manner above mentioned of the terminal cell of the pro-embryo, the first axis of the embryo is formed. In *S. hortensis*, after a very short longitudinal development, the number of the cells of this axis increases no further; on the other hand an adventitious axis shoots out from one of its sides destined to break forth from the prothallium and to produce the first pair of leaves of the embryo (Pl. LVIII, figs. 7—10). The form of the growing end of this shoot, as well as the mode of its cell-multiplication, is exactly that of the subsequent vegetative axes above described. Its growth is directed obliquely upwards. During its longitudinal development, the end of the primary axis of the young plant, which in *S. hortensis* is hitherto hardly perceptible, increases somewhat in size, more by the expansion of its cells than by their multiplication (Pl. LVIII, figs. 7, 10).

Before the shoot of the second order has pierced through the lower, wide-celled layer of the prothallium, it produces two opposite leaves, by the contemporaneous division of horizontal rows of cells of its wide lateral surfaces. After the shoot has emerged to the light these leaves are developed and produce chlorophyll in their cells. The arrangement of their cells exactly corresponds in all stages of development with that of the *primary leaves* of vegetative shoots. In the germ-plants of all the species which I have seen, these leaves bear appendages on both sides of their base. In their axils adventitious leaves are formed, precisely similar to those produced at a later period (Pl. LVII, fig. 22). Not long after the appearance of the first pair of

leaves the naked terminal bud above them becomes forked (Pl. LVII, fig. 22). Now, or soon afterwards, the cells of the lower portion of the axis of the second order undergo a sudden and considerable longitudinal expansion, and thus break through the small-celled upper half of the prothallium. The two leaves spread out expand in length and breadth, and become green.

At the same time the two axes of the third order, into which the end of the axis of the second order has divided, commence their further development. Their cells multiply rapidly in a longitudinal direction, and produce leaves. The four longitudinal rows of leaves do not appear contemporaneously upon the shoots of the third order. A lower first leaf appears without an opposite upper leaf. The next leaf which is a lower leaf of another longitudinal row, is also often without an opposite upper leaf. From thence upwards the arrangement of the leaves is regularly $2\frac{1}{2}$. The longitudinal expansion of the two shoots of the third order (like that of the subsequent vegetative shoots) commences, in *Selaginella hortensis*, for the first time, when their ends begin to fork for the formation of the axis of the fourth order, and the result is that these leaves of the shoots of the third order are for some time so closely crowded, as to appear upon a cursory examination to belong to the axis of the second order, with whose two leaves they seem to form angles of different divergence.

The first adventitious root springs out of that side of the axis of the first order which lies opposite to the place of origin of the shoot of the second order. It corresponds in development and structure most completely with those afterwards produced. In *Selaginella hortensis* it is usually first developed at a very late period, at the time of the commencement of the longitudinal development of the axes of the third order. Exceptions to this are of rare occurrence. It appears much earlier on the germplant of *S. Martensi;* even whilst the embryo remains within the lower layer of the prothallium (Pl. LVII, fig. 20). In the latter species the end of the primary axis is far more fully developed than in the former.

In the mode of cell-multiplication, the succession of the shoots, and the development of the leaves, Lycopodium* comes much nearer to the Polypodiaceæ (for instance to *Aspidium filix-mas*) than to Selaginella. The terminal bud which is a conical wart, extends somewhat beyond the place of origin of the youngest leaf. The division of its apical cell, as well as the multiplication of the cells of the second degree, resembles the same process in Aspidium. The leaf appears to be formed by the multiplication of a single cell of the circumference of the terminal bud. It grows in length by division of an apical cell by septa inclined alternately towards the upper and the under surface of the leaf. Here also it is easily seen that the cells of the base continue to divide long after the multiplication of the cells of the tip of the leaf has ceased. Ramifications of the stem occur by the forking of the terminal bud above the place of origin of the youngest leaf.† The growth of the roots exactly resembles that of the adventitious roots of the Polypodiaceæ, the Equisetaceæ, and the Pilulariæ.

Psilotum triquetrum is exactly like the Selaginellæ in the mode of forking its terminal buds. This plant also resembles *Selaginella viticulosa*, and still more so *S. cordifolia*, in the relation of the annual shoots to the buried perennial stem.

The growth of the stem of Psilotum results from the repeated division of a single apical cell by means of septa inclined alternately in different directions. The growth of the leaves in the first stages of development resembles that of Lycopodium. Afterwards a forking of the tip of the leaf takes place.

The reproduction of those Lycopodiaceæ which bear powdery spores of one kind only is still a mystery. Repeated sowings of the spores of *Lycopodium clavatum*, *L. inundatum*, and of *Selago*, have yielded me no results, but I have lately often observed that in spores of *Lycopodium Selago*, which had been sown for from three to five months, numerous small spherical cells had been formed, similar to

* I have particularly examined *Lycopodium inundatum*.

† Compare Nägeli, 'Zeitschr. f. Botanik,' Parts 3 & 4, Pl. v, fig. 1.

the mother-cells of the spermatozoa of *Selaginella helvetica*. I have not yet found spermatozoa inside these vesicles. De Bary has lately discovered ('Berichte der naturf. Gesellsch. zu Freiburg,' 1858, p. 467), that the spores of *Lycopodium inundatum* produce a body composed of a few cells, whose structure is not unlike that of the archegonium of a fern. It is probable from these observations that the similarly formed spores of Lycopodium, Psilotum, &c., are of different sexes, and as in *Equisetum arvense* produce partly archegonia and partly spermatozoa.

Of late years the Lycopodiaceæ have received less attention from vegetable anatomists than any other of the higher cryptogams. Since the appearance of those parts of Bischoff's 'Cryptogamische Gewachse,' which relate to these plants, few papers on the subject have been published. Karl Müller's observations (which however are full of errors), are to be found in the 'Botanische Zeitung' for 1846, besides which we have Nägeli's work cited above, and Mettenius's history of the origin of the embryo of *S. involvens*. Spring's monograph is devoted principally to the limitation of the species.

CHAPTER XV.

CONIFERÆ.

THE ovules of the Coniferæ, however much they may differ in their position and mode of attachment, exhibit the greatest uniformity in their internal structure. A simple, somewhat fleshy integument, surrounds a short and thick nucleus formed of delicate cellular tissue, leaving open a wide micropyle-canal. In the anatropal ovules of the Abietineæ the division between nucleus and integument extends downwards only for a short distance (Pl. LIX, fig. 10); the mouth of the ovule widens considerably above the apex of the nucleus, parallel to the spermophore, and appears as a transverse fissure. In *Pinus sylvestris* and *P. strobus* the nucleus exhibits a very remarkable depression of its apex; in *Pinus balsamea* (Pl. LIX, figs. 10, 11), the depression is less manifest. The nucleus in Juniperus and Thuja increases in diameter towards the apex: in both, the apex exhibits a depression, which however in Juniperus is but slight (Pl. LXIV, fig. 5). Lastly, the nucleus of Taxus, which is far larger than that of any other indigenous Conifer, is quite like that of most phænogams, in its oval form, and in the separation between its nucleus and integument, which extends to the base of the ovule (Pl. LXIII, fig. 1).

The nucleus at the time of the shedding of the pollen consists of delicate-walled cells filled with granular mucilage. Deep in its interior—in the Abietineæ and in Juniperus, underneath the place where the integuments and the nucleus amalgamate; higher up in Thuja, and still

higher in Taxus—certain of the cells (in the Abietineæ and in Juniperus rarely more than one)* of the middle longitudinal string of the cellular tissue of the ovule become the embryo-sacs (Pl. LIX, figs. 10—12). In the ovule of Taxus a short row of cells, usually consisting of three cells of the axile cellular string of the nucleus, is distinguished from the neighbouring cells by their size, and by their containing an abundance of granular mucilage mixed with small starch-granules (Pl. LXIII, fig. 2). Of these cells sometimes one, sometimes each one of the three is developed into a perfect embryo-sac; Taxus, at first, always exhibits more than one. The cellular layers immediately surrounding the embryo sac are strikingly distinguishable from the rest of the tissue of the ovule by their more delicate cell-walls, and by the greater concentration of the mucilaginous contents.

The first stages of development of the pollen of the Coniferæ, from the individualization of the mother-cells up to that of the pollen-cells, correspond exactly with the ordinary type of phænogams. The young anther of Pinus † appears at the end of the autumn preceding the flowering season as a short, spatula-shaped scale, convex below. On its under-side, near the base, two oval protuberances are to be seen: these are the lobes of the anthers. Each lobe is filled with a firmly-connected tissue of rather large, delicate-walled cells, the mother-cells of the pollen. Each of these cells contains a spherical nucleus, occupying about one half of the cell-cavity, and having rather transparent fluid contents, and several very small nucleoli. The rest of the cell-cavity is occupied by a gelatinous mucilage in which numerous very small starch-granules are embedded. Tincture of iodine colours this mucilage a pale yellow, and the coagulating fluid contents of the nucleus a deep brown. Two layers of tabular cells form the entire outer covering of the mass of mother-cells; the layer of horizontally

* There are trees of *Pinus sylvestris* (one for instance in a marshy spot in the Botanical Garden at Leipzig) which, like the yew, develope two embryo-sacs in most of their ovules.

† The species which I examined were P. sylvestris, maritima, Larix, and balsamea.

expanded cells which occurs in so many monocotyledons and dicotyledons is altogether wanting in the Coniferæ.

The mother-cells remain during the winter in the state described. At the commencement of the warmer season the connexion between the mother-cells is dissolved. This occurs in *Pinus sylvestris* at the beginning, and in *P. maritima* in the middle of April. The membranes of these cells become thickened, and one or two of the nucleoli have increased in size. In *Pinus balsamea* this growth is far more considerable than in *Pinus sylvestris*, where sometimes all traces of the nucleoli have already disappeared. The fluid substance of the nucleus coagulates very easily under the action of water, even more rapidly than in Tradescantia. The viscid fluid contents of the cell then appear most clearly distinct from the spherical cavity, which was filled by the nucleus before the latter became coagulated and contracted into a spherical ball. In *Pinus Larix* the slight tendency of the cell-fluid to absorb water and become swollen—which is the cause of the appearances above mentioned in *P. balsamea*—exhibits itself in a different manner. The membrane of the mother-cell swells rapidly in water, and is lifted away from the cell-contents, the original volume of which is not increased.

The dissolution of the nucleolus or nucleoli soon ensues, as well as that of the nucleus, just in the same way as in Tradescantia, Lilium, Iris, Passiflora, &c. In the homogeneous fluid contents of the cell, two large flattened elliptical nuclei are next formed. The fluid substance of the latter refracts light in almost exactly the same manner as the fluid contents of the cell, from which it can only be distinguished with much difficulty. At their first appearance these nuclei never contain nucleoli (Pl. LIX, figs. 2—4). Nucleoli—especially in *Pinus balsamea*—are first produced at a later period, contemporaneously with the distinct definition of the limits of the cell-fluid. These nucleoli are always very numerous, sometimes there are as many as twenty. The nucleoli produced from the nucleus of a ruptured mother-cell of *P. balsamea* were coloured blue by diluted tincture of iodine, proving themselves to be starch-granules.

The numerous amyloid granules of the cell-sap, accumulate, after the production of two secondary nuclei, in the form of an annular girdle in the equator of the cell. This girdle soon divides into two, parallel to one another (Pl. LIX, fig. 3). The division of the cell-contents into two halves appears thus to be indicated. These conditions are so frequent that I do not doubt they must occur in all mother-cells. The further formation, however, takes place in two different ways. The case of least frequent occurrence is as follows:—A delicate line suddenly appears in the equator of the cell between the two girdles of granules, which line immediately disappears under the action of strong reagents. I believe the line to indicate the surface of contact of the two membraneless halves of the cell-contents produced by the division of the contents of the mother-cell. Shortly afterwards a circular ridge makes its appearance, seated upon the inner wall of the mother-cell and traversing its equator, and forming as it were a frame to the septum of the two special-mother-cells of the first degree which are in course of formation. The other case above alluded to, and which is the one of ordinary occurrence, is the following:—The division of the primordial utricle is interrupted by the fact that the membranes of the secondary nuclei are absorbed, and in the place of each one of them, two—making four altogether—perfectly spherical nuclei are formed, which either lie in one plane, or are arranged at the angles of a tetrahedron. Between each two of these, flattened accumulations of granules are produced, in each of which a delicate line suddenly becomes visible, which is the first indication of the septum dividing the two special-mother-cells.

After the formation of two special-mother-cells of the first degree, two cells are formed in each of them, so that then each set of special-mother-cells consists of four.

Pinus Larix differs somewhat from other Coniferæ in the circumstance that in one way or another more than four special-mother-cells and pollen-cells are frequently, in fact almost always, formed in one mother-cell. The usual number is six, and the occurrence of seven or eight is not unusual (Pl. LIX, fig. 6).

In *Juniperus* and *Thuja occidentalis* the phenomena of cell-division are exactly the same as in the above-named plants. In the former, however, on account of the smallness of all the parts, and in the latter, owing to the abundance of starch-granules in the cell-contents, the observations are rendered much more difficult.

In each special-mother-cell a pollen-cell is formed, which, when its membrane first becomes visible, entirely fills the cavity of the former. The two layers of the membrane of the pollen-cell, the intine and the extine, are clearly distinguishable whilst the pollen-cell is still enclosed in the special-mother-cells. The rudiments of the two hemispherical appendages of the extine which are characteristic of *Abies pectinata*, *Picea vulgaris*, and *Pinus sylvestris*, are formed whilst the pollen-cell is still within the special-mother-cell. These appendages consist, when in the young state, of a soft inner substance, which passes on the outside into a firmer cortical layer composed of reticulate ridge-like protuberances. By the use of any fluid which attracts water, such as a solution of sugar, the inner substance is contracted into a smaller space, and the cortical layer of that portion of the appendages which is furthest from the middle point of the pollen-cell is made to turn inwards.

After the pollen-cells have become free by the dissolution of the walls of the mother- and special-mother-cells, a cell-multiplication commences in them which is quite peculiar to the gymnosperms, and is not seen in any other phænogams. Two nuclei suddenly appear in the cell—a spherical one, similar in all respects to the original nucleus of the pollen-cell, and one somewhat smaller of a very flatly-lenticular form (Pl. LIX, fig. 7). It is hardly a matter of doubt that the latter is newly formed by the side of the primary nucleus of the pollen-cell. Soon afterwards the two nuclei appear separated by a membrane, convex towards the larger one, having the form of a segment of a spherical surface, and which divides the pollen-cell into two unequal parts. That part which contains the flattened nucleus is the smaller one. The disproportion in size of the two parts is inconsiderable in *Pinus Larix* (Pl. LIX, fig. 8), but very remarkable in *Picea vulgaris* and *Pinus sylvestris*.

In the Abietineæ the lenticular daughter-cell of the pollen-grain increases rapidly in size, and divides twice by septa convex towards the middle point of the pollen-cell. When the pollen-grain is ripe a cellular body is found at one end,* projecting far into the cavity of the pollen-grain, and consisting of a large vesicle borne upon a stalk consisting of two low meniscoid cells. In *Pinus Larix* this body fills more than half the cavity, and in *Picea vulgaris* and *Pinus sylvestris* it fills the latter almost entirely (Pl. LIX, fig. 9).

The inner membrane of the pollen-cell exhibits, even in the young state, a great capacity for distension, so that when placed in water the intine swells into a wide layer, which stretches the extine and compresses the cell-contents. After the pollen-grain is ripe this peculiarity is intensified; thus, for instance, when the detached pollen of *Pinus sylvestris* is moistened with water, the extine is immediately ruptured, and frequently entirely stripped off.†

The development of the pollen of Juniperus, Taxus, and Thuja appears to be similar in all respects to that of the Abietineæ, but the smallness of all the parts, and the want of transparency of the cell-contents interferes very much with the examination in these plants. The perfect pollen-grain of Juniperus, Thuja, and Taxus appears to be divided

* That end which corresponds with the point of contact of the pollen-cell with its sister-cell. In *Pinus Larix* the daughter-cell lies in the more pointed end of the oval pollen-cell: in *Pinus sylvestris* and *Abies pectinata* it lies on the longest edge of the pollen-grain, in the middle part of that side which lies opposite to the side which bears the two hemispherical appendages of the extine.

† The structure of the pollen of the Abietineæ was correctly understood and described by Fritzsche ('Mem. Acad. St. Petersbourg p. divers savants,' III (1837), p. 693). He states that at the one pole of the somewhat ellipsoidal pollen-grain of *Pinus Larix*, the outer one of the two layers which compose the inner membrane encloses a cavity filled with granular matter, underneath which, in a depression of the inner layers of the intine, a second similar but more spherical cavity is found; to the latter is attached a closed vesicle, filled with fovilla, which projects into the interior of the pollen-grain. Fritzsche in like manner ascertained the structure of the pollen of *Pinus sylvestris*—a more difficult matter—only here the central vesicle appeared to him to be altogether wanting. Schacht ('das Mikroskop,' 2nd edition, Berlin, 1855, p. 148) explained that in *P. sylvestris* the vesicle in question entirely fills the cavity; he pointed out also that in the Coniferæ it is not the inner membrane of the pollen-grain, but the above vesicle—the terminal cell of the short row of cells which is attached to one pole of the pollen-grain—which grows out and forms the pollen-tube.

into only two unequal cells; it is probable that the larger of the two is the terminal cell—expanded so as entirely to fill the pollen-cell—of the short row produced by the multiplication of the smaller portion of the pollen-grain.*

The cell-multiplication in the interior of the pollen-grain of the Coniferæ takes place very rapidly; in the space of a few days; I observed it, for instance, in *Pinus Larix*, in the year 1855, to last from the 27th of March to the 10th of April.

The pollen of the Coniferæ passes through the wide micropyle directly on to the nucleus. Each pollen-grain sends out into the tissue of the latter—at first only for a short distance—a tube formed by the prolongation of the terminal cell of the short row of cells attached to its inner wall. In Taxus and Juniperus this tube is emitted shortly after the shedding of the pollen, in the Abietineæ not until after remaining dormant for many weeks. The formation of pollen-tubes takes place in *Pinus sylvestris*, *Mughus*, and *austriaca* at the beginning of June, in *P. Strobus* somewhat later. In a few days they penetrate at the utmost not farther than near to the place where the integument separates itself from the nucleus (Pl. LIX, fig. 14); then, and not unfrequently even sooner, their longitudinal growth ends for the first time (Pl. LIX, fig. 17). Up to this point the embryo sac remains a simple cell, whose large nucleus is gradually dissolved (Pl. LIX, fig. 14). Some days later however numerous free nuclei appear in its interior (Pl. LIX, fig. 15), and immediately thereupon it appears filled by a large number of radially-elongated cells arranged in a concentrical layer (Pl. LIX, figs. 16, 16^b), which multiply actively in all three directions until the commencement of the winter rest. The primary wall of the embryo-sac has in the mean time become so thin and delicate that it almost disappears from observation. At the same time a considerable multiplication of all the cells of the nucleus

* The pollen of Ephedra behaves exactly like that of Larix (see Schacht, 'das Mikroskop,' 2nd ed., 1855, p. 148); the pollen of the Cycadeæ on the other hand appears unicellular when ripe. Possibly stages of development similar to those of the Coniferæ are gone through in these plants, but are entirely obliterated at an early period.

takes place in length, breadth, and thickness. With the commencement of the cold season the walls of the endosperm which fills the embryo-sac become much thickened, and exhibit lamination of the gelatinous substance of the thickened portions (Pl. LIX, fig. 13). If delicate sections of the endosperm are placed in water, the gelatinous matter of the thickening layers of the cell-walls becomes rapidly and easily dispersed in the fluid; the primordial utricles of the cells then lie free in the cell-cavity (Pl. LIX, fig. 17). The thickened walls of the central cells of the endosperm are the most sensitive to the action of water. This peculiar nature of the cells of the transitory endosperm of the first year renders the observation of their walls especially difficult.*

At the beginning of March the dissolution of the thickened cell-walls of the endosperm commences. Each of the primordial cells thus made free exhibits a large central spherical nucleus filled with brighter fluid (Pl. LX, fig. 1). About April this nucleus is dissolved; cells whose nuclei have been just absorbed contain numerous spherical drops of a highly refractive substance, which nearly fill the cell. Further developed cells contain two (Pl. LX, fig. 1^b), others four, many only three nuclei. Around each such nucleus a free daughter-cell is formed, originally of a spherical shape, lying free in the mother-cell. By absorption of the wall of the mother-cell the daughter-cells become free; the same process is repeated in their interior (Pl. LX, fig. 3). Thus the number of the cells enclosed by the embryo sac increases very rapidly in geometrical progression. The embryo-sac itself grows in a remarkable manner to more than twenty times its previous volume by pushing aside the loosened cells of the adjoining portions of the nucleus of the ovule; its wall, hitherto very tender, becomes thick and glassy, and ultimately granulated on the outer surface. At the same time a very active mul-

* The earlier observers considered the embryo-sac filled with cellular tissue to be a cavity in the tissue of the nucleus (*Hartig*, 'Naturgeschichte der Forstculturpflanzen,' see the explanation to fig. 17 of Plate XXV. *Gottsche*, 'Bot. Zeit.,' 1845, p. 380). Quite lately Pineau pointed out its true nature ('Ann. d. Sc. Nat.,' iii ser. vol. ii, p. 85).

tiplication recommences in the cells of the ovule, with the exception of the upper portion of it which has been traversed by the pollen-tubes and which remains stationary; the ovule grows from one third of a line to two lines and a half.

In the middle of May a simple layer of cells begins to spread itself on the inner wall of the embryo-sac (Pl. LX, fig. 2). The side-walls of these cells do not yet touch one another at all points (Pl. LX, fig. 2^b); if the embryo-sac is ruptured by gradually increased pressure, the cells within it and those also which are spread over its wall are driven out through the fissure in the form of spherical vesicles (Pl. LX, fig. 3). The firm adhesion *inter se* of the above cells does not take place until after several layers of them have been formed (Pl. LX, fig. 4). The cell-multiplication at the same time goes on continually, both in the free cells of the centre, and in those forming the parenchymatal mass of the periphery. Thus at last there is again formed an endosperm entirely filling the inner cavity of the embryo-sac, a body far longer in its circumference and composed of a far greater number of cells than the one which existed at the commencement of the winter rest. The development of the endosperm of Juniperus much resembles that of the species of Pinus whose seeds take two years to ripen. In the lower part of the nucleus before the shedding of the pollen there is found a cell surrounded by concentrical layers of smaller cells: this cell is the embryo-sac. It becomes filled with a few cells (Pl. LXIV, fig. 5), shortly after those pollen-grains which have reached the nucleus have begun to emit tubes. In this condition the ovule remains through the first summer and winter. At the commencement of the next vegetative period the ovule and embryo-sac increase rapidly and remarkably in size, and the primordial utricles of the cells which fill the embryo-sac become individualised. By active multiplication of these primordial cells, numerous cells are produced floating freely in the fluid contents of the embryo-sac. They soon * clothe the inner wall of the embryo-sac in the form of a compound cellular layer (Pl. LXIV, fig. 6); by division

* At the beginning of May in the second year.

of the cells of the latter, coupled with the deposition of new cellular layers on the inner side of those first formed, the embryo-sac is soon (within the space of a week) filled for the second time with closed cellular tissue.

The development of the endosperm of Taxus is far more simple. The rudiments of the embryo-sacs are here represented (as has been already mentioned) by several larger cells situated in the middle of the lower portion of the nucleus of the ovule, surrounded by cellular tissue arranged in scale-like layers (Pl. LXIII, fig. 2). Soon after the shedding of the pollen the tissue surrounding those cells becomes loosened (Pl. LXIII, fig. 4). The growing embryo-sacs begin to increase considerably in size; this increase in many instances continues to go on in one only of the embryo-sacs; the growth of the others is arrested, they become shrivelled, and at last, like the loosened cells of the surrounding tissue, they are dissolved and displaced by the one embryo-sac (Pl. LXIII, figs. 5—8). Often however two of these larger cells grow and form embryo-sacs. The nucleus of the cell destined to form the embryo-sac is soon absorbed, and the cell then usually assumes the shape of a flask (Pl. LXIII, fig. 5). Two new nuclei soon appear contemporaneously in its upper part, embedded in the mucilaginous layer which clothes the inner wall. More and more nuclei soon make their appearance in the lower part also of the young embryo-sac in a similar position (Pl. LXIII, figs. 6, 7). At first they often have no nucleoli, but at a more advanced period of growth the latter are never wanting. A cell is formed around each of the nuclei which are deposited upon the inner wall of the embryo-sac (Pl. LXIII, fig. 8). The walls of the young cells soon close upon one another, and thus the embryo-sac is filled with closed cellular tissue, except at its young upper end, where nuclei are found which for a long time continue to float freely (Pl. LXIII, fig. 9), until at last, at this end also, the formation of parenchyma proceeds. In those Abietineæ whose seeds ripen the first year, the embryo-sac is filled, a few days after the shedding of the pollen, with a closed tissue of large cells (Pl. LXII, fig. 11), by whose continual multiplication in all three directions the endosperm

increases in size. Thuja and Cupressus behave in just the same manner.

In all the Coniferæ, after the embryo-sac has become entirely filled with cellular tissue, a considerable growth commences in certain cells situated close under the micropylar end of the endosperm, which growth sets in even long before the cell-multiplication in the neighbouring cells has ceased (Pl. LX, figs. 5—7). Thus the essential part—viz., the large spherical cell—of the so-called corpuscula is differentiated from the surrounding tissue. In the Abietineæ each corpusculum is separated from the next by at least one, often by several cellular layers (Pl. LX, figs. 6, 7; Pl. LXII, fig. 3). The corpuscula of Juniperus (Pl. LXV, figs. 1—3, 9), Thuja and Cupressus, immediately adjoin one another. In Taxus two corpuscula are sometimes in contact; most of them are separated from one another by thick layers of cellular tissue (Pl. LXIV, figs. 1, 2).

The corpuscula of Taxus are shortly ellipsoidal, those of the Abietineæ are ellipsoidal and elongated; those of Juniperus and Cupressus are long and prismatic, with blunt edges and small ends. The formation of corpuscula is not always limited to the micropylar end of the albuminous body. In Juniperus especially, numerous irregularities occur: sometimes there is only a remarkable increase in size of the deeply seated cells of the endosperm, sometimes a corpusculum is formed complete in all its parts and opening in the middle of one of the lateral surfaces of the endosperm.

The apex of each corpusculum is at first only separated by a single cell from the inner wall of the upper arch of the embryo-sac. In most of the Coniferæ this cell divides twice, and produces four cells lying in one plane which are distinguished from the neighbouring cells by their contents being thickly mucilaginous and having many granules; this is the case in *Pinus sylvestris* (Pl. LX, fig. 8), *Pinus Strobus*, *austriaca*, *maritimus* and *Mughus*; in *Abies Larix* and *balsamea*; in *Taxus baccata* (Pl. LXIII, fig. 11), and *canadensis* (Pl. LXIV, fig. 1); in *Juniperus sibirica* (Pl. LXV, figs. 2, 9) and *communis*; in *Cupressus pyramidalis* and *Thuja orientalis*. In *Pinus Fraseri* I found the four apical

cells often divided transversely, so that the rosette consisted of eight cells lying in two planes. *Pinus canadensis* and *Picea L.* are remarkable exceptions. Here the one cell which covers the top of the corpuscula does not divide by longitudinal septa crossing one another, but by repeated transverse septa (Pl. LXII, figs. 1, 2). It thus keeps pace with the multiplication of the cells of the top of the endosperm, which multiplication in the other Abietineæ and in Juniperus continues after the formation of the corpuscula, whilst in the above species the double pairs of cells which cover the upper arch of the corpuscula are sunk in depressions of the upper side of the endosperm, over which the primary membrane of the embryo-sac extends. In Juniperus, Thuja, and Cupressus the top cells of all the corpuscula, with rare exceptions, are closely crowded together at the base of a wide depression of the top of the endosperm (Pl. LXV, figs. 2, 9). The upper end of the endosperm of Pinus exhibits as many funnel-shaped depressions as there are corpuscula; each of these short passages leads to a single corpusculum. In like manner, in Juniperus, Thuja, and Cupressus, the parenchyma of the endosperm grows over the covering cells of the corpuscula. At the top of the endosperm there is found a rather deep depression whose base is occupied by the closely-crowded four-celled rosettes of the elongated corpuscula, which latter are in contact with one another.

The cells of the endosperm which adjoin the corpusculum on the sides and below, divide repeatedly by septa at right angles to the surface of the latter. A layer is thus formed which surrounds the corpusculum, and consists of small cells filled with granular mucilage. This layer is very striking in the Abietineæ.

In *Pinus sylvestris* and *austriaca* the number of corpuscula is from three to five; in *Abies balsamea* and *pectinata* usually three; in *Pinus canadensis* very regularly four (rarely five); in *Taxus baccata* and *Juniperus* from five to eight.

The primary nucleus of the cell which becomes the corpusculum lasts for some time; in *Pinus sylvestris* (Pl. LX, figs. 5, 6) until the corpusculum has attained half its full

size; in Juniperus (Pl. LXV, fig. 2) until the full size is attained. In Pinus it usually lies at the upper end of the corpusculum—that end which is turned towards the micropyle—rarely at the opposite end; it is embedded in a mucilaginous layer, which clothes the inner wall of the organ, and which in Pinus is thin, and rendered turbid by numerous granules (Pl. LXV, figs. 5, 6), and in Juniperus and Cupressus* firm and transparent; in the centre of the corpusculum there is only a small ellipsoidal cavity filled with watery fluid. At last the nucleus is dissolved; in *Pinus sylvestris* this is often preceded by the formation of a free spherical cell around this nucleus† (Pl. LX, fig. 5). At last it disappears from observation, and at the same time, in the Abietineæ, several vacuoles make their appearance: the latter are so numerous and so close together in *Pinus sylvestris* and *Strobus*, that they impart a frothy aspect to the whole contents of the corpusculum; in *Pinus Laricis* and *canadensis* they are less numerous and of very unequal size. During the further development of the corpuscula the number of these vacuoles diminishes. Nuclei and free nucleolate spherical cells now appear amongst them, the latter at first being only small and few in number. Their number however soon increases, whilst that of the vacuoles diminishes more and more. In *Pinus sylvestris* and *Strobus*, and in *Abies Laricis*, the latter disappear entirely before the arrival of the pollen-tube at the corpusculum, whilst in *Pinus canadensis*, *Picea Laricis*, and in Larix, one or two of the vacuoles in the middle of the corpusculum usually last until the moment of impregnation. In *Pinus canadensis*, *Picea Laricis*, and Larix, the free cells which float in the interior of the corpuscula, *i. e.*, the germinal vesicles, appear almost all undivided until impregnation (Pl. LXII, fig. 1); in a few cases only in *Pinus canadensis* and *Laricis*, individual germinal vesicles are found more or less entirely filled

* In the later stages of development of the corpusculum; in the earlier condition strings of granular mucilage radiate from the nucleus.

† As is the case round the primary nucleus of the embryo-sac of *Asphodelus luteus* and *Funkia cærulea*. See pp. 10 and 13 of my 'Entstehung des Embryo der Phanerogamen.'

by two, very rarely three or four, endogenous daughter-cells. In *Pinus sylvestris* on the other hand very many of the germinal vesicles, and in *Pinus Strobus* almost all of them, contain, even before impregnation, several—sometimes as many as six, usually four—nucleolate daughter-cells. The membranes of the germinal vesicles, as well as those of the daughter-cells formed before their impregnation, dissolve in water. The germinal vesicles of *Pinus canadensis* contain small amyloid granules which are not found in other species. The phenomena which may be observed in the formation of the germinal vesicles, resemble generally those which appear in the formation of the cells of the endosperm of phænogams in the restricted sense of the word. The free cell-formation in the impregnated embryo-sac of the Irideæ* offers the most points of resemblance. As in that case the first organized formations have the form of vesicles of moderate size. They either possess fluid contents only, or in more rare instances they have one or two spherical bodies (nucleoli) of a strongly refractive substance, floating in the fluid contents. These formations according to current notions must be considered as nuclei. The larger of these vesicles exhibit in their interior a small spherical, cellular formation—the nucleus around which the cell originated—situated somewhat excentrically, and exactly similar to the above-mentioned freely-floating bodies. There is only one circumstance which does not entirely accord with these explanations of the observations, and that is, that sometimes (although not often), cells are found whose single nucleus is decidedly smaller than any one of the freely-floating nuclei observed contemporaneously in the same corpusculum. This may however very probably depend upon individual peculiarities. It may well be, that the moment at which a cell is formed round a nucleus, is determined by circumstances quite unconnected with the fact whether or not the nucleus has attained its greatest size. A nucleus might, long before it was full-grown, become the middle point of a cell in process of formation. If it be

* 'Entstehung des Embryo,' p. 27.

assumed that its growth then ceased, the above phenomenon would be sufficiently explained.*

The refractive power of the substance of the nuclei of the freely-floating cells of the corpuscula of *Pinus sylvestris, austriaca,* and *Strobus,* is so exactly the same as that of the contents of the cells, that the nuclei do not become visible until by the prolonged action of water, or of tincture of iodine, the contents of the cell and of the nucleus are changed, and the albuminous matter coagulated. In the corpuscula of *Pinus canadensis* the refractive power of the nuclei upon transmitted light is greater than that of the contents of the cells.

The number of the freely-floating cells in the corpuscula of the Abietineæ is so great that they quite fill the latter. This is the ground of the statement made by Mirbel and Spach that the corpuscula are filled "par un tissu fin et jaunâtre." In Taxus, Juniperus, and Cupressus, the number of these cells is usually less, but yet cases occur here also in which they entirely fill the corpuscula (Pl. LXIII, fig. 11; Pl. LXIV, fig. 1; Pl. LXV, fig. 9).

Of the many delicate-walled daughter-cells of the corpusculum, those which occupy its upper and lower end often appear to be pressed against it, in like manner as the germinal vesicles of the phænogams and the cells antipodal to them press against the two ends of the embryo-sac. In the upper end of the corpusculum they are only found when the arch of the latter is particularly steep, and then several usually occur (Pl. LXI, fig. 1); in the lower end one only is found, and that not often; when present it is much flattened above.

The development of the endosperm in the embryo-sac of the Coniferæ does not appear to be absolutely dependent upon the contact with pollen of the same species, although

* It is undeniable that *many* cases of free cell-formation, especially those occurring in the embryo-sac of phænogams, when considered by themselves, agree better with the theory of the identity of the cell and the nucleus, than with the opposite one propounded by Schleiden. It is not so however with all; in some cases (*Asphodelus albus, Staphylea pinnata*) the diameters of the cells in process of formation are always at least half as large again as those of the largest of the freely-floating nuclei. The undoubted analogy however with the fully-observed cases of the so-called cell-division, suggests the necessary explanation even of those more obscure phenomena.

it is undeniably favoured by such contact. I have known flowers of female specimens of *Juniperus sibirica*, which had been completely separated from male ones, to produce normal fruit, and to develope endosperm with fully formed corpuscula. Female flowers of young trees of *Pinus canadensis*, which were three miles distant in a straight line from the nearest other trees of the same species, produced, for two years successively, only female flowers, but no male ones. Microscopical examination showed that in both cases no pollen-grains were present upon the nucleus. In both, the formation of embryos was entirely suppressed.

After the interval which occurs in the growth of the pollen-tubes—and which takes place even in those Coniferæ whose seeds ripen the first year—the latter begin again to penetrate towards the embryo-sac. This happens almost at the time when the differentiation of the corpuscula from the surrounding tissue commences. After the tubes are completely formed they reach the endosperm: in *Pinus sylvestris* and *Juniperus sibirica* this happens at the beginning of June, in *Pinus Strobus* and *Juniperus communis* at the end of June of the second year; in *Abies excelsa* and *Taxus canadensis* in the middle of May, in *Taxus baccata* at the end of May, and in *Pinus canadensis* at the end of June, of the first year. The deeper the pollen-grains penetrate into the nucleus the thicker they become, a phenomenon which is most manifest in Taxus, and least so in the Abietineæ. The growth in thickness of the lower part of the pollen-tube of Taxus is so remarkable, that the organ assumes the form of a conical sac (Pl. LXIII, fig. 11; Pl. LXIV, figs. 1, 2). The great transverse increase does not commence until the completion of the longitudinal growth.

About the time when the pollen-tube reaches the endosperm, the very thick, hitherto leathery and tough primary wall of the embryo-sac which encloses the endosperm, is softened at the top. The pollen-tube breaks through this wall, apparently after some resistance, (a constriction or sudden narrowing of the tube is often visible at this place), and reaches the double pairs of cells which cover the tops of the corpuscula. Sometimes it makes its way sideways to the corpusculum, piercing through and destroying the

tissue of the endosperm. This has been often observed in *Pinus canadensis*. In Taxus it often destroys the entire uppermost part of the endosperm; on the other hand the four cells which close up the corpusculum which is about to be impregnated, are at first only slightly pushed apart from one another, by the protrusion by the pollen-tube of a short prolongation which passes between their detached edges and up to the outer wall of the corpusculum (Pl. LXIV, figs. 1, 2). These cells do not disappear until a later period, after the formation of the pro-embryo; they often last for a very long time (Pl. LXIII, fig. 13). Juniperus and Thuja (Pl. LXV, figs. 2, 3, 9, 10,) behave in a similar manner. In the Abietineæ, on the other hand, the cells above the corpuscula are destroyed immediately after the pollen-tube has reached them (Pl. LX, fig. 9; Pl. LXI, fig. 1; Pl. LXII, figs. 2, 3). Its end attaches itself to the outer wall of the corpusculum; in *Pinus canadensis* it then often expands considerably in breadth (Pl. LXII, fig. 3). With this process in most cases, its penetration terminates; more rarely it breaks through the wall of the corpusculum and grows into it for a short distance. This happens regularly in *Pinus Larix*, and tolerably frequently in *Pinus canadensis* (Pl. LXI, figs. 13, 14; Pl. LXII, fig. 2).*

Free spherical cells are often developed in the interior of the ends of those pollen-tubes of the Coniferæ which penetrate up to, or into the corpusculum. In the Abietineæ the observation of them is often rendered difficult by the large number of co-existent starch-granules, but even here undoubted instances of the presence of cellular formations in the pollen-tubes may easily be seen. The pollen-tube of *Pinus canadensis* when it has penetrated into the corpusculum usually contains—in addition to granules of starch and mucilage—several (2, 4, or even 8) sharply defined spherical balls of finely granular protoplasm floating freely in the interior of the tube (Pl. LXIII, fig. 2). In some of these corpuscula I saw, close under the end of the pollen-tube but not in contact with it, a free oval cell differing from the germinal vesicles which—still in the same state as before the arrival of the pollen-tube—filled the rest of the

* Many such cases are figured by Pineau, 'Ann. d. Sc.' iii. sér.; vol. xi, pl. vi, fig. 4; and by Schacht, 'Entw. des Pflanzen-embryon,' pl. xi, fig. 5—7.

cavity of the corpusculum, by being somewhat larger, and especially by its containing a considerable quantity of granules of protoplasm of a larger size (Pl. LXII, fig. 2). The nucleus of these cells differs from those of the neighbouring germinal vesicles by the more considerable size of the nucleoli. In other corpuscula which were taken partly from ovules of the same cone I found a similar cell, but without a nucleus, at the base of the corpusculum. In other corpuscula, again, from the same inflorescence, a cell of the same kind furnished with a firm membrane* was firmly pressed into the lower end of the corpusculum. It can now be recognised beyond a doubt as the primary cell of the compound pro-embryo (Pl. LXII, fig. 4). In an impregnated corpusculum of *Pinus canadensis* which already contained a multicellular pro-embryo, I once saw a large free cell, situated above the latter and containing two nuclei, and very similar to an impregnated germinal vesicle on the point of dividing (Pl. LXII, fig. 5). This observation is the only one of the kind which occurred in the course of my very numerous investigations, and it indicates that more than one germinal vesicle of the same corpusculum may be impregnated.

The pollen-tube of *Pinus sylvestris*, after penetrating the rosette of the corpusculum, usually passes only for a short distance into the interior of the latter, so that the end of the tube projects into the end of the cavity in a hemispherical form; a farther penetration is of rare occurrence. In the earliest observed conditions in which a change in the contents of the corpusculum was perceptible, an oval, capacious, sharply defined cell, was visible near the base of the corpusculum; in the more pointed lower end of this cell a lenticular nucleus was embedded in a considerable accumulation of granular protoplasm (Pl. LX, fig. 9). The walls of the upper part of the cell are clothed with a thin layer of plasma; a flattened layer of protoplasm passes through the entire length of the upper cavity of the cell. In other corpuscula the lower end of this cell almost touched the base of the corpusculum. In these cases the nucleus, and the accumulation of protoplasm enclosing it, appeared sur-

* In the conditions previously mentioned this membrane was wanting.

rounded by a firm cell-wall, and separated from the upper, very delicate-walled, larger un-nucleated portion of the cell. Corpuscula from the same tree examined one or two days later, exhibited this small lower daughter-cell attached to the lower part of the corpusculum, to whose walls the lateral surfaces also of the upper, un-nucleated, larger portion of the cell adhere, whilst the boundary in the direction of the apex of the corpusculum becomes indistinct (Pl. LX, fig. 10). As in *Pinus canadensis* the end of the pollen-tube during these processes exhibits no opening; its contents are of the same nature as in the species just mentioned. The unimpregnated germinal vesicles which fill the cavity of the corpusculum remain at first unaltered, which is also in accordance with *Pinus canadensis*. A difference, however, exists in *Pinus sylvestris*, viz., that very often one or two of the germinal vesicles which lie in the micropylar end of the corpusculum and touch the end of the pollen-tube, have firm membranes composed of cellulose, a fact which has never been observed in *Pinus canadensis*. After the cell which is pressed into the lower end of the corpusculum has become changed by repeated divisions into the compound pro-embryo, the tip of the pollen-tube of *Pinus sylvestris* often appears to be open, and its contents to be discharged into the cavity of the corpusculum; this is plainly the result of mechanical rupture. The cells of the endosperm which surround the funnel-shaped depression leading to the corpusculum expand considerably in width after impregnation, and compress the pollen-tube, frequently to such an extent as to obliterate the cavity of the latter. Its contents thus undergo a strong pressure, which must ultimately lead to the rupture of the free end.

In *Pinus abies*, *L.* (*Abies excelsa*, *D. C.*), I observed phenomena similar to those in *Pinus sylvestris*. In some cases I saw the daughter-cell of the corpusculum —after the former had grown to a large size, and its contents had increased and become firmer—in immediate contact with the end of the pollen-tube (Pl. LXI, fig. 1). In others I found a similar but very large cell half way towards the base of the corpusculum divided into four

cells, forming two larger upper ones and two smaller terminal cells (Pl. LX, figs. 2, 2^b.) The identity of this cellular body with the compound pro-embryo which is afterwards firmly inserted into the lower part of the corpusculum is beyond all doubt. In *Pinus Abies* the germinal vesicles, which remain in contact with the end of the pollen-tube, regularly become clothed with firm elastic cell-membranes.

The pollen-tube of *Pinus Larix* usually swells out in a vesicular manner within the funnel-shaped depression of the endosperm above the corpusculum, and then sends forth a pointed prolongation, which pierces through the covering cells of the latter. The membrane of the tube is incomparably more tenacious than in the above-mentioned species. In the latter when the endosperm is detached from the nucleus the pollen-tube regularly tears off at the place where it emerges from the tissues of the nucleus, whilst in *Pinus Larix* the apex of the pollen-tube may often be drawn out from the corpusculum, so as to hang freely down for a considerable distance.

The end of the pollen-tube even before it reaches the corpusculum exhibits an accumulation of protoplasm which is often sharply defined like a cell, and further upwards in its interior numerous starch-granules are seen partly combined in groups of twos or fours. Immediately after reaching the corpusculum the apex of the pollen-tube, when drawn out from the latter, appears rather thin-walled and without appendages. In cones somewhat more developed a cell is found fastened to the end of the pollen-tube when the latter is detached. The diameter of this cell seldom equals that of the end of the pollen-tube, and often remains considerably less. It resembles in all its parts one of the smaller germinal vesicles which float in the interior of the corpusculum. Like these vesicles it exhibits a nucleus of lighter substance, and is devoid of the firm cell-membrane.* No further change is at this time perceptible in the remaining portion of the corpusculum.

* At the place where this cell is attached, the pollen-tube exhibits no trace of an opening, and there is nothing to show that the cell, which differs so remarkably from the pollen-tube by the absence of a firm membrane, has grown out of the latter.

In corpuscula which are about two days more advanced a larger cell is seen near the end of the pollen-tube which now reaches down into the corpusculum; this larger cell differs from the neighbouring unaltered germinal vesicles in its circumference—which is more than double that of the latter—in its more transparent fluid contents, and in its firmer membrane. Its upper end not unfrequently protrudes above the spot at which the before-mentioned small cell is attached to the apex of the pollen-tube. The large free cell never exhibited any connexion with the small cell. In other corpuscula of the same cone a larger cell of the same kind occurs at the base of the corpusculum. Its circumference is more considerable, and its contents of the same kind, as in the above-described impregnated germinal vesicles of *Pinus sylvestris*. The more pointed lower end of the oval cell is filled by an oval daughter-cell with turbid contents and a firmer membrane. The larger upper part of the cell is devoid of a nucleus; a thin protoplasmic layer covers the inner wall, and a similar flattened layer traverses the inner cavity longitudinally (Pl. LXI, fig. 13). A short time afterwards the lower cell, which is rich in granular protoplasm, appears pressed into the base of the corpusculum (Pl. LXI, fig. 14). It is now drawn out breadthwise; its upper wall, which is turned towards the inner cavity of the corpusculum, is only slightly arched. Observation shows that it is the rudimentary cell of the compound proembryo. The upper unnucleated portion of the large cell becomes attached laterally to the arch of the corpusculum, but is soon dissolved.

The free germinal vesicles in the upper part of the corpusculum continue in the mean time without any observable alteration (Pl. LXI, fig. 14). On the other hand, the cell attached to the tip of the pollen-tube becomes clothed with a firmer membrane of cellulose at the time when the large transparent cell appears near the tip of the pollen-tube; sometimes also it increases in size so that its transverse diameter becomes three times that of the pollen-tube (Pl. LXI, figs. 12—14). The inner wall of the pollen-tube exhibits, exactly at the point where the cell is attached to it, a narrow pit traversing the thickening layers which

in the mean time have been deposited upon its wall (Pl. LXI, fig. 12). This pit always appeared to be closed on the outside by the primary membrane of the pollen-tube; no open communication between the pollen-tube and the cell could be ascertained. The nucleus of this cell has by this time disappeared; its contents, which are tolerably transparent, are only rendered turbid to a certain extent by a few fine granules. Sometimes it contains some larger bodies, equal in size to the starch granules in the pollen-tube, and composed of a substance rendered brown by iodine. The relations of position between the cell and the pollen-tube are of two kinds: either the upper part of the cell is attached to the terminal point of the extended conical tip of the pollen-tube, and thus hangs down freely into the cavity of the corpusculum (Pl. LXI, figs. 13, 14), or else the end of the pollen-tube is lifted up round the cell—so as to form an annular cushion—and grows round the larger part of the cell so as only to leave the hemispherical lower end protruding out of the introverted end of the pollen-tube (Pl. LXI, fig. 11). This process has been observed in its different stages. If a moderate pressure is applied to the upper end of a pollen-tube having the attached cell enclosed in the introversion of its apex (Pl. LXI, fig. 11), the introverted membrane often becomes exserted, and the exserted portion then appears to be conical, and bears the cell in question at its outermost tip (Pl. LXI, fig. 11), just as in the first case above described. The two forms of the end of the pollen-tube are equally common in longitudinal sections of corpuscula. In isolated instances two such cells are attached to the tip of the pollen-tube.

From these observations on the Abietineæ I think the following conclusions may be drawn as to the development of the embryo. After the arrival of the end of the pollen-tube *at* or *into* the upper end of the corpusculum, one of the germinal vesicles lying near the end of the pollen-tube is impregnated. It increases in size, and glides through the mass—consisting of protoplasm and unimpregnated germinal vesicles—which fills the corpusculum, down to the base of the latter, into which it presses itself. At this time (in *Pinus canadensis*) or, (in *P. sylvestris* and *Laria*) even

during its downward progress, a daughter-cell is formed in its lower end, by the repeated bipartition of which, the compound pro-embryo originates. It always happens in *Pinus Larix*, and frequently in *P. sylvestris*, that one or more of the germinal vesicles which are in contact with the pollen-tube, but which remain unimpregnated, acquire firm membranes of cellulose, and attach themselves to the tube, but this phenomenon is not essentially connected with impregnation.*

The swelling which the pollen-tube of *Taxus baccata* forms above the top of the endosperm often attains dimensions equalling that of the latter. Where much pollen has fallen, several pollen-tubes almost always penetrate into the ovules. These tubes swell and press against one another, so that they not only fill the entire cavity above the endosperm, but pass beyond it, sending forth prolongations of different forms. Cases occur in which the swollen ends of numerous pollen-tubes grow round the endosperm on all sides, and meet underneath it, thus smothering it by cutting off the access of nutriment. Even before the corpuscules are fully developed one, or more rarely two, large spherical cells are formed in each pollen-tube. These cells have no firm membranes, and are filled with a thickly-fluid finely-granular protoplasm which encloses a central nucleus. These cells at first float quite freely in the interior of the pollen-tube. They are often surrounded by a

* Schacht ('Beiträge zur Anatomie,' &c., Berlin, 1854, p. 287, 'Das Mikroskop,' 2nd edit., Berlin, 1855, p. 151, 'Flora,' 1855) arrived at a conclusion to some extent in accordance with the above, inasmuch as it assumed the descent of the rudiment of the pro-embryo from the upper end of the corpusculum to the lower. In the 'Flora' for 1855 I have attempted to show that Schacht's conclusions are incorrect. The objects which he took for the rudiments of the pro-embryo cannot in the nature of things be what he supposed.

Geleznoff's statements as to the formation of the embryo of Larix are more opposed to mine. He considers that the cell attached to the pollen-tube grows by degrees out of the apex of the latter, and he assumes that the two communicate by an open pore, and that the first cell of the pro-embryo originates in the lower end of this cell. In all these points my observations gave a negative result. I believe that I may place great reliance upon them, not only on account of my investigations having been carried on for three years, but because my numerous observations were repeated and verified during a sojourn in the Alps, where, from the opportunities which existed for collecting cones at places of different altitudes, the various stages could be followed out much more easily and with greater certainty than could be done in a flat country.

thin layer of granular mucilage, from which fine strings radiate to the walls of the tube. In more advanced ovules these cells appear to be situated nearer to the lower wall of the pollen-tube, and to be fastened to the latter by an accumulation of viscid protoplasm; their earlier spherical form has passed into a flatly-ellipsoidal one. Instead of the central nucleus, which has now disappeared, two newly-formed nuclei make their appearance, one in each focus of the cell (Pl. LXIII, fig. 11).

The unimpregnated corpuscula usually contain only a few (from six to ten) free germinal vesicles, amongst which one in particular, which floats in the middle part of the corpusculum is distinguished by its size, by the sharpness of its outline, and by the richness of its granular contents (Pl. LXIII, fig. 11).*

The prolongation of the pollen-tube which penetrates between the cells of the rosette of the corpusculum is frequently, but not always, filled by four cells placed crosswise, manifestly produced by the twice-repeated division by means of longitudinal septa of the (originally) free spherical cell which is now adherent to the inner wall of the tube (Pl. XLIV, fig. 2). One of the germinal vesicles in the interior of the corpusculum, apparently the central one, now appears swollen, as well as more rich in granular contents, and in many instances situated nearer to the base of the corpusculum (Pl. LXIV, fig. 2). The membrane of the pollen-tube when uninjured appears completely closed. The openings which are sometimes seen in it after its separation from the corpusculum are almost certainly accidental ruptures. The contents of the four cells which fill the pollen-tube, or of the *one* cell which is sometimes found there, consist of very small motionless bodies, partly spherical and partly spindle-shaped, which fill the cell in great numbers. The next condition of the impregnated corpuscula exhibits the impregnated germinal vesicle at the base of the latter, firmly pressed into the lower end of the

* In the 'Vergl. Unters.,' p. 129, I took this formation to be the primary nucleus of the corpusculum. This I think was an error, because in the Abietineæ and Juniperineæ the nucleus of the corpusculum does not last until impregnation.

corpusculum (Pl. LXIV, fig. 1). The unimpregnated germinal vesicles remain still unchanged in the upper part of the corpusculum.* Sometimes one or two of the impregnated germinal vesicles which are in contact with the pollen-tube become clothed with firm cellulose membranes, and adhere to the apex of the tube.

The side-walls of the upper end of the corpuscula of *Thuja orientalis*, *Juniperus communis*, and *J. sabina* are considerably thickened, and furnished with delicate annular ridges, which are often very clearly visible in the form of transverse stripes. At the beginning of July the contents of the corpuscula consist, as has been mentioned, of very finely granular almost glass-like transparent protoplasm in the middle of which a large vacuole occurs. Above this vacuole the primary spherical nucleus of the corpusculum lies embedded in the protoplasm. This nucleus afterwards disappears, and in its place some new free nuclei make their appearance, around which, in a short time, spherical cells are formed, which are the germinal vesicles. Whilst the latter continue to grow, the central vacuole becomes perpetually smaller and smaller: at last it disappears altogether, and the corpusculum is filled with a uniform mass of protoplasm having the germinal vesicles floating in it. Amongst the latter, one or more near the upper end of the corpusculum are distinguished by their great size (Pl. LXV, fig. 9 *on the right*).

The pollen-tube breaks through the softened membrane of the embryo-sac—which membrane extends over the depression at the top of the endosperm—and becomes swollen so as to entirely fill the depression. In the regular course of things a large spherical cell now appears in the interior of the pollen-tube, filled with granular mucilage which surrounds a central transparent nucleus (Pl. LXV, fig. 9). In certain conditions which must doubtless be looked upon as more advanced, this cell has the form of an ellipsoid, and is furnished with two nuclei, one in each focus; other conditions again exhibit the cavity of the cell traversed by a septum passing between the two

* A decisive proof that the pollen-tube does not, as Schacht supposes, entirely fill the corpusculum ('Flora,' 1855).

nuclei. Ultimately, and shortly before the pollen-tubes penetrate into the rosettes of the corpuscula, two spherical cells of the kind above mentioned (Pl. LXV, fig. 9 *on the left*) are often found in the tube, which in all probability are produced by the division of the original single cell. The increasing pollen-tube now presses together the rosettes of the corpuscula, and sends a short, very delicate-walled prolongation through the line of contact of the four cells which are in process of dissolution, into each corpusculum which is to be impregnated (Pl. LXV, figs. 3, 10). In some cases the free cells contained in the pollen-tube now appear to be much flattened, attached to the wall of the tube, and divided into a larger number, normally sixteen, of small cells lying in one plane (Pl. LXV, fig. 4); in other cases the pollen-tube contains four middle-sized, or eight smaller, roundish cells, without any firm membrane (Pl. LXIV, fig. 3), and which probably have arisen from repeated division of one of the large originally spherical cells. The protruded portion of the pollen-tube breaks through the compact membrane of the upper end of the corpusculum, forming a fissure which is very visible in the apical aspect of the latter. Even after impregnation, the ends of the tubes if carefully extracted appear quite closed (Pl. LXV, fig. 10). In an object so delicate as the membranes of these tubes, a small opening might easily be overlooked. The following observation, however, is decisive as to the non-existence of any such opening: the contents of the corpuscula, especially of those of *Juniperus sabina* and *communis*, when just impregnated, swell up after imbibing water, and rupture the wall of the corpusculum. If a longitudinal section of the endosperm of a germinal vesicle which has just been impregnated, is placed under the microscope, it will be seen that as the contents of the corpusculum swell, the delicate-walled prolongation of the pollen-tube which reaches into the upper end of the corpusculum is intersected and ultimately ruptured, whereupon an active current begins to flow out of the corpusculum into the pollen-tube. Frequently, but not always, one of the round cells in the pollen-tube forces its way into the prolongation which is sent out by the membrane

of the latter into the corpusculum which is to be impregnated. These cells, which now become very easily disintegrated, contain numerous spindle-shaped motionless bodies, consisting of a substance coloured brown by iodine. These bodies are short in Thuja and elongated in Juniperus (Pl. LXIV, fig. 3^b).*

The first change which is visible in the corpusculum after the entry of the pollen-tube, is an increase in the granular matter contained in the larger germinal vesicle. This cell gradually moves towards the lower end of the corpusculum, against which it ultimately presses itself (Pl. LXV, fig. 10). The larger germinal vesicles which lie in its way are displaced and dissolved; the smaller ones remain unaffected. Since any successful longitudinal section through the endosperm of an impregnated germinal vesicle lays bare many different stages of development of neighbouring corpuscula, there cannot, in the great number of cases which are brought into comparison, be any doubt as to the order of their succession. Even in Juniperus, especially in *Juniperus communis*, the smaller impregnated germinal vesicles which are immediately attached to the end of the pollen-tube, very often possess firm membranes composed of cellulose.

In all the Coniferæ the impregnated germinal vesicle, which is pressed into the bottom part of the corpusculum, divides by a transverse septum, so far that is as this division has not already taken place during its descent. The two daughter-cells—of which the upper is the larger one and the lower more rich in protoplasm—divide by longitudinal septa: in some cases this division occurs only in the lower one (Pl. LX, fig. 11; Pl. LXI, figs. 3—7). Shortly afterwards the septum which divides the upper, more empty cell or cells, from the rest of the cavity of the corpusculum, is dissolved. The two longitudinal portions of the lower daughter-cell of the germinal vesicle form the first rudiment of the pro-embryo of the Coniferæ. Its formation is always

* It might easily be imagined that the cellules produced in the interior of the ends of the pollen-tube of Coniferæ might produce spermatozoa. My observations however have hitherto only yielded negative replies to the question, as will be seen by the account given above.

the same, even in species which differ widely as to the period of development.

In the Abietineæ both the cells—whose form is that of the longitudinal moieties of a blunt cone, with a convex basal surface—either divide again immediately by *longitudinal* septa at right-angles to the one last formed (Pl. LX, figs. 11, 12; Pl. LXI, fig. 3), or else a division first occurs in each of them by *transverse* septa perpendicular to the longitudinal axis of the corpusculum, by which the cells are divided into two very unequal portions, the upper one being much the largest. In the lower, smaller ones of the newly-formed cells, which contain much more concentrated mucilage than the upper ones, the division by *longitudinal* septa then ensues, which latter septa are perpendicular to the septum dividing the two cells (Pl. LXI, fig. 6). The latter phenomenon is the most common.

The pro-embryo now consists of two pairs of two-celled, parallel rows of cells, having their edges of contact rectangular. The number of its cells is increased by repeated division of each of the (lower) terminal cells by means of septa at right-angles* to the longitudinal axis of the organ. It is a rule without exception that the lower of the newly-formed cells are the smallest, but the richest in formative matter. The pro-embryo up to this time occupies only a proportionably small space, filling the lower part (a tenth to a fifth part) of the corpusculum. As the development of the pro-embryo has stretched the lower part of the corpusculum downwards whilst its upper part remained stationary, the portion of the corpusculum which is filled by the pro-embryo bears a much larger proportion to the upper part, than the portion occupied by the germinal vesicle when first impregnated. The pro-embryo exhibits no upward growth. The lateral walls of its uppermost oldest cells are as intimately amalgamated with the inner wall of the corpusculum as the thickening layers of the same wall are with one another.

* Speaking more accurately we might say, transverse septa radial to the inner wall of the corpusculum. They are often strongly inclined downwards from the longitudinal axis of the pro-embryo, and are thus convex upwards (pl. lx, fig. 13; pl. lxi, fig. 16); the position at right angles to the axis of the organ is first assumed by them after the subsequent longitudinal and transverse expansion of the latter.

In the upper part of the corpusculum the numerous spherical sister-cells of the germinal vesicle are still distinctly perceptible (Pl. LX, fig. 13; Pl. LXII, fig. 5). From the fact of their presence* it is impossible that the opinions of Schleiden, Schacht, and Geleznow, as to the process of embryo-formation in the Coniferæ can be correct. According to the two former the pollen-tube penetrates into one of the corpuscula, fills it up by degrees entirely, and produces the pro-embryo in its lower end, which is pressed against the inner surface of the corpusculum. If this were so, the pollen-tube must pierce through the mass of spherical cells which fills the cavity of the corpusculum before impregnation. Nothing however is easier than to see that those cells are still present when the pro-embryo appears. They are only dissolved very gradually, and become changed, together with the rest of the contents of the upper part of the corpusculum, into a yellowish grumous mass.

The increase in length of the pro-embryo ultimately ruptures the base of the corpusculum. A considerable longitudinal expansion immediately takes place in the two pairs of cells of which it consists; this expansion usually occurs in the second cell reckoned from above (Pl. LXI, fig. 7; Pl. LXII, fig. 8), but sometimes the first expands also. The lower end of the pro-embryo is thus driven deeply into the tissue of the endosperm underneath the corpuscula. The axile cells of the middle portion of the endosperm become in the mean time loosened and softened, by which the course of the continually-descending end of the pro-embryo is pointed out beforehand. The courses of the continually-elongating pro-embryos through the pultaceous mass of the softened cellular tissue, form delicately-winding spirals.

Soon afterwards the longitudinal rows of cells comprising the pro-embryo become detached from one another. The separation commences at the lower end and progresses from thence upwards (Pl. LXI, figs. 9, 10). During this breaking up of the pro-embryo into four (very rarely more than four) simple rows of cells, the four shorter cells which formed its upper end which was enclosed by the corpusculum, become dissolved (Pl. LXI, figs. 8—10).

* Observed by Gottsche ('Bot. Zeit.,' 1844, 509), and by Pineau, 'Arm. d. Sc. Nat.,' 3rd ser., vol. ii.

Shortly after the rows of cells of the pro-embryo have separated from one another, the formation of the embryo itself commences in the terminal cell of each row, either immediately, or after the occurrence of divisions by horizontal septa. This formation takes place by the repeated division of the apical cell for the time being by means of septa inclined in the first place alternately to the right and to the left, and soon afterwards in three different directions. The cells of the second degree divide into inner and outer cells by radial, and those of the third degree by longitudinal septa parallel to the axis, and so on, following the mode of cell-multiplication in the terminal bud of Equisetum and other plants (Pl. LXI, fig. 11; Pl. LXII, figs. 9, 10). In the half-ripe seed the number of rudimentary embryos is at least four times as great as that of the corpuscula impregnated. Of these however, in the greater number of cases, one only is developed rapidly and vigorously; the rest are much less fully developed, shrivel up by degrees, and ultimately die. During the formation of the embryo the younger lower cells of the pro-embryo—which latter has become the suspensor—also expand considerably in length, and at last the same expansion occurs in its massive portion immediately adjoining the embryo (Pl. LXI, fig. 10; Pl. LXII, fig. 10). The latter also then become disconnected from the laterally-adjoining cells (Pl. LXII, fig. 10), and often, especially near the lower end, bear a deceptive resemblance to a pro-embryo not yet broken up into its longitudinal rows of cells.*

After the penetration of the pro-embryo into the middle region of the endorsperm, the walls of the corpusculum can easily be separated from the surrounding tissue. They exhibit now prominent reticulate ridges on the outer side, corresponding in direction with the edges of contact of the neighbouring cells, and they have also somewhat large flat pits. These phenomena are especially manifest in *Pinus canadensis* (Pl. LXII, fig. 8). In this species the upper portion of the four uppermost cells of the pro-embryo are normally much thickened, and then exhibit manifest lamination (Pl. LXII, fig. 7); sometimes strange-shaped

* It is doubtless from this phenomenon that some observers, especially Geleznow, deny the breaking up of the pro-embryo into distinct suspensors.

accumulations of gelatinous matter are found on the outer walls of these cells (Pl. LXII, fig. 8).

I have never seen the pollen-tube ramify in the Abietineæ. Each pollen-grain sends forth only one tube; if several corpuscula of the same ovule are to be impregnated, it is indispensable that several pollen-tubes should reach the nucleus. There is no ground for assuming an incapacity for impregnation in any of the different corpuscula of the same endosperm. The impregnation of all the corpuscula of one endosperm, when not exceeding three in number, happens not unfrequently in *Pinus sylvestris* and *canadensis*, each being acted upon by a special pollen-tube. In Taxus the impregnation of several corpuscula by the very widely expanded end of a single pollen-tube, is of very frequent occurrence; and in Juniperus and Thuja it is the rule.

The impregnated germinal vesicle of *Taxus baccata* and *canadensis* divides frequently by longitudinal septa before any increase takes place in the number of its cells in a longitudinal direction. The pro-embryo not unfrequently consists of only four longitudinal rows of cells, but usually of six (Pl. LXIII, fig. 12). In the longitudinal development of the pro-embryo its rows of cells behave very differently. In some, multiplication and growth cease at a very early period; it usually happens that the upper end of the pro-embryo exhibits some three-sided cells which renew themselves rapidly downwards, and belong to no one of the longitudinal rows underneath, of which the pro-embryo is composed. Very commonly two or one of the longitudinal rows of cells immediately adjoining the longitudinal axis of the pro-embryo are more vigorously developed and multiply their cells in a longitudinal direction more rapidly, than the cells nearer to the periphery (Pl. LXIII, fig. 13). The pro-embryo does not break up into single rows of cells until a later period, and then usually only partially. Normally one only of them goes beyond the first commencement of embryo-formation.*

* 'Hartig zur Entwickelungsgesch. d. Pflanzen,' Leipzig, 1844, fig. 25, and Schacht (l. c. pl. ix, figs. 11, 13) represent the first stage of development of the pro-embryo as an oval mass of parenchymatal cellular tissue. I cannot confirm this; the pro-embryo appeared to me, even in its earliest youth, to be always clearly composed of longitudinal rows of cells.

The impregnated germinal vesicle—which is pressed into the lower end of the corpusculum— of *Juniperus communis* and *sabina*, as well as that of *Thuja orientalis*, divides by a transverse septum into two daughter-cells (Pl. LXV, fig. 10), of which the lower one frequently encloses the larger portion of the protoplasm of the mother-cell. The upper wall of the upper cell is usually soon dissolved (Pl. LXI, fig. 4); when it lasts longer (as is often the case) the same vigorous downward expansion which takes place after some time in all the cells of the pro-embryo, takes place also in the uppermost of the two cells of the rudimentary pro-embryo (Pl. LXV, fig. 3).* The farther development of the daughter-cell of the impregnated germinal vesicle resembles, in its essential features, that of the Abietineæ. It divides by longitudinal septa, and the elongated daughter-cells divide by transverse septa, which latter division is repeated in the terminal cells. The number of longitudinal divisions of the second cell of the pro-embryo is however far less definite than in the Abietineæ. The most usual number of the rows of cells of the pro-embryo is four, but pro-embryos are also often found which consist of only two or—on account of the longitudinal division of one of the latter—of three longitudinal rows of cells (Pl. LXV, fig. 4).

These rows of cells very soon become disconnected after the pro-embryo has broken through the base of the corpusculum. Their longitudinal expansion is still more remarkable than in the Abietineæ (Pl. LXV, fig. 5). If after the last transverse division (Pl. LXV, fig. 6) of the terminal cell of one of the detached rows of cells, the formation of the embryo commences by the production of differently inclined septa in the lower one of the newly-formed cells, then the lower end of the last cell of the pro-embryo, upon which the embryo is seated, grows very

* These enlarged upper portions of the impregnated germinal vesicle exhibit a very large nucleus with proportionably large nucleoli. The occurrence of the division of the germinal vesicle into an upper and a lower portion, of which the latter is destined for more active further development, the former remaining stationary, and sometimes containing a nucleus, sometimes not—brings to mind the similar phenomena in Gagea and Fritillaria ('Entstehung des Embryo,' pp. 20, 21).

considerably in breadth (Pl. LXV, figs. 7, 8). In Juniperus also all the numerous young embryos usually miscarry, except one.

The stages of development of the embryos of the Coniferæ which follow next after the impregnation of the germinal vesicle, are passed through with just as much rapidity as contemporaneity. A very short time, scarcely twenty-four hours, elapses between the arrival of the end of the pollen-tube at the upper end of the corpusculum of the Abietineæ, and the formation of the four-celled compound pro-embryo at its base; and these processes of development occur almost contemporaneously in all ovules of all trees of the same species growing under similar circumstances. Thus in 1854 I found that on the 22nd of June, near Leipzig, no single pollen-tube of *Pinus sylvestris* had reached a corpusculum; whereas only three days later, on the 25th of June, there was only one amongst several hundreds of impregnated corpuscula which I examined, whose impregnated germinal vesicle was not already divided into four cells. In Taxus and the Juniperineæ the contemporaneity of the development is less complete; here we find different stages of development extending over about eight days, consisting of germinal vesicles unimpregnated, impregnated and unicellular, or impregnated and multicellular, all near one another.

Robert Brown* was the discoverer of the poly-embryony of the Coniferæ. In a later treatise† (1834) he pointed out the origin of the pro-embryo in large cells of the endosperm, to which he gave the name of corpuscula. Corda‡ first proved that the pollen-tubes penetrate into the interior of the corpuscula. Schleiden,§ in 1843, gave the first accurate account of the nature of the pro-embryo. As many subsequent observers have done, he mistook the

* 'Ann. d. Sc.' 1st ser., vol. viii, p. 211.

† 'Ann. d. Sc.' 2nd ser., vol. xx, p. 193.

‡ 'Nova Acta,' vol. xvii, p. 599. Upon other points this work is of no use.

§ 'Grundzüge,' 1st edn., vol. ii, p. 375. R. Brown's account of the young pro-embryo is incomplete. He figures (l. c., vol. xx, pl. v, fig. 9) a pro-embryo whose smaller terminal growing cells are torn off.

pro-embryo for the embryo. Hartig* was the first to observe that the upper part of the suspensor is a single row of cells. He had not a clear idea of the relation of the suspensor to the pro-embryo. Mirbel and Spach† discovered the breaking up of the pro-embryos into single rows of cells in Pinus, Thuja, and Taxus. Gottsche's‡ excellent work contains the most careful *critique* of the then known facts, and the first accurate description of the structure of the corpuscula of Pinus; it also gives a renewed and complete proof of the advance of the pollen-tube to the corpuscula, as well as proof of the fact that the rudiment of the pro-embryo is visible in the lower end of the corpusculum, whilst the sister-cells of the germinal vesicle are still present.

The greater part of the above investigations were undertaken in the years 1848 and 1849.§ I have already mentioned their agreement with Pineau's views, and their divergence from those of Geleznow and Schacht.

* 'Naturgeschichte der Forstcultur pflanzen,' Erklärung zur Tafel, XXV.
† 'Ann. d. Sc. nat.,' ii Sér. vol. xx, p. 257.
‡ 'Bot. Zeit.,' 1845, 377.
§ Read at the August sitting of the Leipzig Natural History Society.

CHAPTER XVI.

REVIEW.

THE comparison of the development of the mosses and liverworts on the one hand, with that of the ferns, Equisetaceæ, Rhizocarpeæ, and Lycopodiaceæ on the other, discloses the most complete uniformity between the fruit-formation on the one hand and the embryo-formation on the other. The structure of the archegonium of the mosses—the organ within which the fruit-rudiment is formed—is exactly similar to that of the archegonium of the vascular cryptogams, the latter being that part of the prothallium in the interior of which the embryo of the frond-bearing plant originates. In both the large groups of the higher cryptogams there is a cell which originates freely in the larger central cell of the archegonium, by the repeated division of which (free) cell, the fruit of the moss and the frond-bearing plant of the fern are produced. In both, the divisions of this cell are suppressed and the archegonium miscarries, unless, at the time of the opening of the top of the latter, spermatozoa find their way to it.

Mosses and ferns therefore exhibit remarkable instances of a regular alternation of two generations very different in their organization. The first generation—that from the spore—is destined to produce the different sexual organs, by the co-operation of which the multiplication of the primary mother-cell of the second generation, which exists in the central cell of the female organ, is brought about. By this multiplication a cellular body is produced which in the mosses forms the rudiment of the fruit, and in the vascular cryptogams, the embryo. The object of the

second generation is to form numerous free reproductive cells—the spores—by the germination of which the first generation is reproduced. The leafy plant in the mosses answers therefore to the prothallium of the vascular cryptogams; the fruit in the mosses answers to *the fern* in the common sense of the word, with its fronds and sporangia. The pro-embryo, that is to say the confervoid process produced by the germinating spore of most of the mosses and many of the liverworts, cannot be looked upon as a special generation any more than the similar organ (the suspensor) in phænogams. It is to be remembered that when new individuals are produced from single cells of the leaf of a moss, and also during the development of the gemmæ of many mosses, the formation of the rudiment of the first leafy axis is preceded by the formation of a similar confervoid pro-embryo. This holds good as well in the mosses * as in those liverworts which possess a pro-embryo. When new individuals are formed from the fragment of a leaf of *Lophocolea heterophylla* or of *Radula complanata*, the cell of the surface of the leaf which becomes the mother-cell of the new plant produces in the former of the above-named plants a single or double row of cells, and in the latter a cellular surface. In each case the body produced is exactly similar to the pro-embryo which originates from the germinating spore in both species.

The vegetative life of the mosses is confined exclusively to the first, and the fructification to the second generation. The leafy stem alone sends forth roots: the spore-forming generation draws its nourishment from the first generation. The life of the fruit is usually much shorter than that of the leaf-bearing plant. In the vascular cryptogams this state of circumstances is reversed. It is true that the prothallia send out capillary roots: this is always the case in the Polypodiaceæ and Equisetaceæ, and frequently in the Rhizocarpeæ and Selaginellæ. But the prothallium lives a much shorter time than the leaf-bearing plant, which latter in most cases does not produce fruit for several years.

* W. P. Schimper's excellent work, 'Recherches sur les mousses,' renders it unnecessary for me to cite examples.

The contrast however is not so marked as it appears at first sight. The apparently unlimited life of the leaf-bearing moss depends merely upon continual renovation. Phenomena of a similar kind are met with in the sprouting prothallia of Polypodiaceæ and Equisetaceæ. In the lowest liverworts (Anthoceros and Pellia) the structure of the fertile shoots is less complicated, and their duration little longer, than that of the fruit. On the other hand the ramification of the prothallium of the Equisetaceæ is very variable; its life is not of shorter duration than that of an individual shoot.

It is a circumstance worthy of notice that in the second or spore-forming generation of mosses and ferns, complicated thickenings of the cell-walls usually occur (witness the teeth of the peristome in mosses, the capsule-wall and the elaters in liverworts, and the vessels in ferns), whilst in the first generation these thickenings are rare and exceptional.

An unprejudiced consideration of the subject will show that the separation into two groups only of the plants comprising the mosses on the one hand; and the liverworts (Jungermanniæ, Marchantieæ, Anthoceroteæ, and Ricciеæ) on the other, is not natural. There is no marked feature by which these two groups can be distinguished. It is true that a pro-embryo like that in the mosses is wanting in most of the genera of liverworts, especially in all the leafless ones. Many leafy Jungermannieæ, however, especially the true Jungermanniæ, exhibit the phenomenon of the conversion of the germinating spore into a single row of cells, one of which cells, by repeated divisions in all three directions of space, becomes the rudiment of the leafy axis. This phenomenon is as well marked as in any of the mosses. The outward form of the antheridia and archegonia in the two groups differs very slightly. The first stages of development of the fruit-rudiment of the mosses on the one hand and the Jungermanniæ on the other, are, it is true, very different. In the former the longitudinal growth is caused by the continually repeated division of a single conical apical cell of the organ, by means of septa inclined alternately in two directions; in the latter this

growth is caused by the repeated division by horizontal septa, of four cells constituting the upper end of the fruit-rudiment. But the normal mode of cell-multiplication in the fruit-rudiment of the Marchantieæ (including the Targionieæ), and of the Riccieæ, coincides exactly with that of the mosses. Lastly Anthoceros exhibits a form of cell-multiplication of the endogonium which is the same as that of the punctum vegetationis of the ends of the axes of a great number (probably the majority) of phænogams. The septa produced in the one apical cell of the organ, are inclined in regular succession towards the four points of the compass. The presence or absence of a columella, or of elaters in the ripe fruit, are points of no characteristic value; Anthoceros has the columella, but this genus and the Riccieæ have no elaters. Radula in the Jungermannieæ has a vaginula, and so has Anthoceros.

Upon instituting a closer comparison between the mode of development of different forms, four types soon become conspicuous, around which all the phenomena hitherto sufficiently investigated may be conveniently arranged. We thus arrive at the following equivalent groups, which are not however equally rich in the number of genera and forms.

1. Mosses according to the ordinary limits of the family, including the Sphagnaceæ.

2. Jungermannieæ; in which the leafy ones are connected with the leafless ones by a succession of intermediate stages.

3. Marchantieæ, Targionieæ and Riccieæ; all intimately connected with one another by the similarity of the earliest conditions of the fruit, as well by many vegetative phenomena.*

4. Anthoceroteæ.

The mode in which the second generation originates from the first is much more various in the vascular cryptogams than in the others. All ferns however agree in the

* As for instance the precisely similar succession of the shoots; the separation of the tissue of the shoots into an upper layer with intercellular cavities, and a lower layer without cavities; the occurrence of peculiar thickenings upon the inner wall of the capillary roots, &c.

fact that the first axis of their embryo has only a very limited longitudinal development; it is an axis of the second order which breaks through the prothallium and becomes the principal axis; and they all agree further in this, that the end of the axis of the first order never forms the root. All vascular cryptogams are without main roots; they have only adventitious ones.

In more than one respect the formation of the embryo of the Coniferæ is intermediate between the higher cryptogams and the phænogams. Like the primary mother-cell of the spores of the Rhizocarpeæ and Selaginellæ the embryo-sac is one of the axile cells of the shoot, which in the one case becomes converted into the sporangium, in the other into the ovule. In the Coniferæ also the embryo-sac soon becomes free from any mechanical connexion with the surrounding cellular tissue. The filling of the embryo-sac by the endosperm may be compared with the production of the prothallium of the Rhizocarpeæ and Selaginellæ. The structure of the corpuscula bears the most striking resemblance to that of the archegonia of the Salviniæ, and still more of the Selaginellæ. Irrespective of the different mode of impregnation—which in the Rhizocarpeæ and Selaginellæ takes place by free spermatozoa, and in the Coniferæ by a pollen-tube, in the interior of which spermatozoa are probably formed—the transformation of the germinal vesicle into the primary mother-cell of the new plant in the Coniferæ and the vascular cryptogams, only differs in the fact, that in the latter there is usually one single germinal vesicle only, whilst in the former there are very numerous germinal vesicles, of which, normally, one only is impregnated. The embryo-sac of the Coniferæ may be looked upon as a spore remaining enclosed in its sporangium; the prothallium which it forms does not come to the light. In order to reach the archegonia of this prothallium the impregnative matter must make itself a passage through the tissue of the sporangium.

Moreover, the development of the pollen of the Coniferæ, when dispersed, varies in a marked manner from that of phænogams, and exhibits vital phenomena similar to those met with in the microspores of Pilularia, Salvinia, and

Isoetes. The extinction of its sexual function (the protrusion of the pollen-tube) is preceded by a cell-formation in its interior, of which no instance is to be found amongst monocotyledons and dicotyledons.

Two of the phenomena which have led me to compare the embryo-sac of the Coniferæ with the large spores of the higher cryptogams, is common to the embryo-sac of phænogams, viz., the origin of the ovule from an axile cell, and the want of connexion with the adjoining cellular tissue. This is very remarkable in the Rhinanthaceæ on account of the independent growth of the embryo-sac. The Coniferæ are closely allied to the phænogams in the fact that their pollen-grains develope tubes.

The phænogams therefore form the upper terminal link of a series, the members of which are the Coniferæ and Cycadeæ, the vascular cryptogams, the Muscineæ, and the Characeæ. These members exhibit a continually more extensive and more independent vegetative existence in proportion to the gradually descending rank of the generation preceding impregnation, which generation is developed from reproductive cells cast off from the organism itself. The closing members of this series, the Characeæ, pass through their entire vegetative development in this generation, whilst the vital phenomena of the generation which follows impregnation are limited to the filling with oil and starch of the newly formed cell in the central cell of the fruit-branch or archegonium. The development of the latter generation in the Muscineæ is far more important, although in some instances, as for example in Riccia, it is very limited in comparison with the first generation, that namely which precedes impregnation.* This state of things is reversed in the Ferns, the Equiseta, and the Ophioglosseæ. From the Characeæ up to these orders, there is an uncer-

* Anthoceros—which in the development of the second generation stands very low in the scale—exhibits a remarkable analogy with the Characeæ, in the fact that, as in the latter, the formation of its antheridia commences by the growing out of the cells of the wall of an intercellular cavity. The well-known red globules of Chara are manifestly states of antheridia. Cavities communicating with one another are formed round the middle point of the hitherto solid globular mass of cells, within which cavities the antheridia—or cellular threads in whose joints the vesicles which produce the spermatozoa are formed—become developed.

tainty in the different species as to the sexual function of the reproductive cells which are cast off from the organism itself, viz., the spores. In these orders species nearly allied to one another are partly monæcious and partly diæcious. Certain species amongst the Charæ, Muscineæ, the Ferns, and the Equiseta,* produce both kinds of sexual organs, archegonia and antheridia, upon the same individual of the generation preceding impregnation: the latter are always produced before the former. In other Characeæ, Muscineæ and Equiseta, the male and female sexual organs are distributed upon different individuals—a separation which is very complete in certain species of mosses, and not in others. The spores from which, in the Characeæ, Muscinæ, and Equiseta, diæcious prothallia are developed, exhibit no indication of the sex of the individual to be produced from them. But there is often a marked difference in the complete form between the male and female individuals: the former are much smaller than the latter; they are dwarfish. Extreme instances of this are to be found, amongst mosses, in *Dicranum undulatum* and *Hypnum lutescens*. In the Equiseta also the male prothallia are always smaller than the females.

Lastly, the reproductive cells of the *Rhizocarpeæ*, *Isoetes*, and *Selaginella* exhibit, according to their sex, the most remarkable differences in their mode of development, size, and form, so long as they continue in vital connexion with the organism belonging to the generation following impregnation. In the Coniferæ the reproductive cells differ in their origin and formation but little from those of phænogams; they differ only in the nature of the vegetative growth subsequent to their formation—which growth in the Coniferæ is in a high degree independent—in the formation of the row of cells in the interior of the pollen-grain, as well as in the formation of the endosperm, and of the corpuscula in the interior of the embryo-sac.

There are so many essential points of agreement between the Coniferæ and the phænogams, that it is more to the point to get rid of the marked differences in their respective

* The greater number of the Charæ and Muscineæ, a few only of the Equiseta, and all the known forms of Ferns and Ophioglosseæ.

processes of embryo-formation, than to indicate in what they agree. One of these differences is the cell-formation inside the pollen-grain, but the principal one is the development of the endosperm and of the corpuscula, a process exactly analogous to the formation of the prothallia and archegonia of the vascular cryptogams, and which is entirely wanting in the phænogams. The whole series of developmental processes which occur in the Coniferæ between the filling of the embryo-sac with the cellular tissue of the endosperm and the production of the germinal vesicles in the corpuscula, is entirely passed over in the phænogams. Here the germinal vesicles are formed immediately in the embryo-sac. In the phænogams there is no vital phenomenon analogous to the development of the prothallia and of the endosperm of gymnosperms, just as in the cryptogams and the Coniferæ there is no analogue to the endosperm-formation which takes place in so many phænogams after the arrival of the impregnating organ at the embryo-sac. The breaking up of the pro-embryo of the Coniferæ into a number of independent suspensors is a phenomenon of the most peculiar kind, to which nothing amongst the vascular plants bears any resemblance,* and to which the division of the spore (*i. e.* the mother-cell of the oospores) of Fucus into several cells capable of impregnation and development† is hardly analogous, inasmuch as with the latter process the impregnation of the free spore commences and forthwith terminates.

The observations contained in the following note are the result of investigations made subsequently to those detailed in Chapter III. These inquiries have led to the conclusion that Frullania—and probably also *Lophocolea bidentata* and

* The formation of the pro-embryo of *Loranthus europæus* out of four longitudinal rows of cells may be looked upon as a slight indication of this. One only of these cells, the terminal cell, becomes transformed into an embryonic globule. (Hofmeister, in 'Abh. Kön. Sächs. Ges. d. Wiss.,' vi, 543.

† Thuret, 'Ann. d. Sc. Nat.,' iv Sér., 1854, p. 273.)

Ptilidium ciliare—must be excluded from the category of plants having a two-edged terminal cell of the stem.

Note on the Cell-multiplication of the Apex of the Stem in the Leafy Jungermanniæ.

The end of the stem in vigorous shoots of *Jungermannia bicuspidata* exhibits, when viewed from above, a three-sided apical surface of the terminal cell, and an arrangement of the cells adjoining the latter, which leads to the conclusion that the cells of the second degree are formed by the production of septa in the apical cell parallel to each one of the three plane lateral surfaces. The order of succession of the cells of the second degree represents a spiral. All those Jungermanniæ which I examined which had inferior leaves, and consequently trilinear phyllotaxis, exhibited a similar state of circumstances—for instance, *Alicularia scalaris, Calypogeia Trichomanes, Lepidozia reptans, Frullania dilatata, Madotheca platyphylla.* The same was the case also with another Jungermannia—besides *J. bicuspidata*—with bilinear-leaves, viz. *Plagiochila asplenioides.* In the latter—as in *J. bicuspidata*—a leaf originates out of each cell of the two longitudinal rows of cells of the second degree which are turned upwards towards the creeping stem. Each of the cells of the longitudinal row of cells of the second degree which occupies the under surface of the stem, developes from its fore-edge a transverse row of two- or three-celled hairs with elongated clavate terminal cells, which hairs soon fall off.

EXPLANATION OF THE FIGURES.

PLATE I.

ANTHOCEROS LÆVIS.

FIG.

1. Germ-plants seen from above, × 15.*
2. Shoot of a plant cultivated for some time in a room under a hand-glass, × 15.
3. Longitudinal section through an actively growing shoot, perpendicular to the surface. The contents are only shown in the cells of the fore-edge. The youngest cell of the second degree belongs to the upper side of the shoot. The fore-edge of the shoot is surrounded by a layer of mucilage, hardened on the outside, to which grains of dust and sand adhere. × 300.
4. A similar preparation. The section has passed through three archegonia in process of development. × 300.
5. A young shoot seen from above, × 300.
6. Fore-edge of a half-developed shoot in the epidermal cells of which the final division is going on, × 300.
7. A young shoot; on the right and left of the middle shoot are the two rudimentary lateral shoots, seen from above. × 300.
8. Transverse section of a delicate young shoot, × 200.
9. Cells of the interior of a perfect shoot cut through longitudinally, and which, abnormally, contain two chlorophyll-granules, × 300.
10. Portion of a section perpendicular to the surface of a perfect shoot, treated with caustic potash, × 300.
11. Portion of the inner tissue of a longitudinal section of a perfect shoot. One of the cells—that one whose contents are figured—shows the commencement of the formation of a gemma. × 300.
12. A further developed gemma cut through parallel to the surface of the shoot in which it was formed, × 300.
13. A gemma which has sent out a capillary root whilst still within the decaying tissue of the mother-shoot, × 100.
14. Chlorophyll-bodies from one of the cells of the wall of a young fruit, × 400.

* "× 15" means "magnified 15 diameters," and so on all through the figures.

FIG.

14^{b}. A similar body in the act of dividing, × 400.

15. A young archegonium with the adjoining tissue, cut through longitudinally, × 300.

16. An archegonium more fully developed, after the formation of the germinal vesicle in the basal cell, × 300.

17. Portion of a longitudinal section of a shoot perpendicular to the surface, bearing an archegonium just impregnated. A bud which has been cut through is seen in the tissue underneath. × 300.

18. Longitudinal section of an archegonium (with the adjoining cells) with a bicellular fruit-rudiment, × 300.

18^{b}. The mouth of the latter seen from above, × 300.

19. A similar preparation with a multicellular fruit-rudiment, × 300.

20$_{a}$. A 3-cellular fruit-rudiment, detached, × 300.

20^{b}. The same preparation turned round 90°, × 300.

21^{a}. Longitudinal section of a further developed fruit-rudiment, × 300.

21^{b}. The apex of a detached fruit-rudiment, similarly developed, seen from the outside, × 300.

21^{c}. Optical section of the preparation in the same position, × 300.

21^{d}. Optical section of the same after being turned 90° round its longitudinal axis.

22. Longitudinal section of a further developed fruit-rudiment, × 250.

23^{a,b}. Optical longitudinal sections of the upper end of a more advanced fruit-rudiment. The position of 23^{b} differs from that of 23^{a} by a revolution of 90° round the longitudinal axis. × 250.

24. Transverse sections of a similar fruit-rudiment, × 80.

25. Apex of a slightly more developed fruit-rudiment, separated from the lower portion by a transverse section, and seen from above, × 150.

PLATE II.

1. Longitudinal section of a young fruit-rudiment enclosed by the surrounding tissue, × 150.

2. Longitudinal section of a further developed condition of the same parts. A large cavity filled with mucilage has been formed above the apex of the fruit-rudiment. Some of the cells of the wall have grown out into multicellular hairs. × 120.

3. Upper portion of the wart-like protuberance (above the upper surface of the stem) by which the young fruit is enclosed; cut off so that the upper end of the fruit is visible. The cells of the jointed hairs which traverse the mucilaginous mass in the interior of the cavity above the fruit, have already become detached. × 100.

4. Longitudinal section of the upper end of a fruit at the moment of breaking out from the sheath. Only the mucilaginous mass and the dry cellular tissue covering it are shown in detail; the fruit and the sheath are only in outline. × 200.

5. Longitudinal section of a half-developed fruit just after breaking forth from the tissue of the stem, × 100.

FIG.

5^b. The cast-off calyptra (consisting of the ruptured portion of the tissue of the stem, which covered the cavity, together with the mucilage which filled the latter), seen from below, × 100.

5^c. Some of the cells of the edge of this calyptra, × 300.

PLATE III.

1. Columella and right-hand longitudinal moiety of the lower part of a young fruit, the place at which the separation of the grand-mother-cells from the surrounding tissue commences, × 250.
2. Transverse section (high up) of a young fruit, × 100.
3. Spore-mother-cells, just detached, × 250.
4, 5 and 5^b. Spore-mother-cells during the formation of the two secondary nuclei, × 250.
6. A similar cell after the formation.
7 and 8. The same cells during the dissolution of these nuclei.
9. Spore-mother-cell after the formation of the four tertiary nuclei, × 250.
10. The same shortly before the commencement of division, showing the beginning of the swelling of the cell-membrane.
11. Spore-mother-cell (after the dissolution of the primary nucleus) in alcohol and water, which makes the cell-membrane swell, × 750.
12. Spore-mother-cell at the commencement of division, examined in alcohol, × 750.
13. A similar preparation after treatment with water, which makes the cell-membrane swell, × 750.
14. Spore-mother-cell in alcohol before the termination of the division. The course of the edges of the septa—which do not yet reach the middle point of the cell—upon the inner side of the cell-membrane is shown in the drawing. × 750.
15. An abnormal spore-mother-cell, × 250.
16. Longitudinal section, perpendicular to the surface, of the end of a shoot which bears a group of rudimentary antheridia, × 300.
17. Optical longitudinal section of two young antheridia, × 150.
18. Optical transverse section of one of these antheridia, × 150.
19, 20. Optical longitudinal section of more-developed antheridia, × 300.
21. Longitudinal section of an almost ripe antheridium, × 300.
22. Two mother-cells of spermatozoa, each containing a spermatozoon, × 500.

PLATE IV.

PELLIA EPIPHYLLA.

1. Longitudinal section of a ripe spore, × 300.
2. Sketch of a ripe spore in which the outlines of the cells only are shown.

FIG.

3. A ripe spore beginning to germinate, three days after sowing, × 300.

5—9. Germinating spores more developed; six days after sowing, × 100. Fig. 6 is fig. 5 turned round 45°; fig. 7 is the same object turned round 90°; fig. 8 turned round 270°.

10. A germinating spore whose first capillary root is just breaking through the exosporium, × 300.

11—14. Sections of spores more advanced in germination; figs. 11 and 14 seen from above, figs. 12 and 13 from the side. Figs. 11—13 are magnified 300, fig. 14, 150 times. Figs. 13 and 14 represent spores eleven days after sowing.

15. Fore-end of a somewhat more developed germ-plant, 36 days after sowing, seen from above, × 200.

16. Longitudinal section of a similar fore-end, × 200.

17. Fore-end of a germ-plant 42 days after sowing, × 200.

18. Germ-plant 49 days after sowing, × 30.

19—22. Half-developed spring shoots of fertile specimens, × 5.

23. Half-developed spring shoot seen from above, × 200.

24, 25. Longitudinal section, perpendicular to the surface, of half-developed shoots of fertile plants—fig. 24, × 200; fig. 25, × 400.

26, 27. Longitudinal section, perpendicular to the surface, of young shoots of barren plants, × 200.

28. Transverse section of an older shoot of a barren specimen which bears four rudiments of adventitious shoots. Very delicate fungoid threads are seen upon the outer surfaces of the epidermal cells of the mother-shoot. × 200.

29. Longitudinal section of a rudimentary antheridium, × 300.

30. Longitudinal section of an unusually slim antheridium almost ripe. The contents of the cells, and the mother-cells of the spermatozoa, are not shown, × 200.

31$^{a, b}$. Mother-cell of spermatozoa from an unripe antheridium, × 600.

32$^{a, b}$. The same after its escape from a ripe antheridium. The included spiral spermatozoon is already revolving. × 600.

33$^{a, b, c}$. Free spermatozoa, killed by iodine. In 33^{c} and 33^{c} the mother-cell is attached to the hinder end. × 600.

PLATE V.

PELLIA EPIPHYLLA.

1. Vertical longitudinal section of a shoot bearing the rudiments of archegonia, × 30.

2. A similar shoot with more developed archegonia, × 30.

3. Longitudinal section of a very young archegonium, × 400.

4. Longitudinal section of the upper end of a somewhat more developed archegonium, × 300.

FIG.

5. A young archegonium at the time of the dissolution of the transverse septa of the cells of the axile cellular string, × 300.
6. Longitudinal section of an archegonium fit for impregnation, × 200.
6^b. Transverse section of the neck of a similar archegonium, × 200.
7. Similar view of an archegonium ready for impregnation and of a very young one similarly magnified, × 200.
8. Three-celled fruit-rudiment, detached, × 300.
9^a. Group of three archegonia impregnated artificially, with two young abortive archegonia, × 40.
9^b. Young fruit-rudiment, longitudinal section.
10. Longitudinal section of a more developed fruit-rudiment, × 300.
11. Longitudinal section of a young fruit, showing the commencement of the separation of the tissue of the interior of the capsule (about the 20th August), × 150.
12. Primordial utricle of a cell of the interior of a capsule in the same state of development, set free by the dissolution of the swollen substance of the wall, × 200.
13. Longitudinal section of a further developed fruit, × 40. In part of the interior of the capsule the arrangement of the elaters and spore-mother-cells is visible (middle of September).
14. Spore-mother-cell with protrusions (one turned away from the observer) of the wall; on the 8th of September. × 500.
15. The same, in which the cell-contents are not shown, × 500.
15^b. The same, turned round 90°, × 200.
16. Mother-cell with four protrusions (one turned away) answering to the special-mother-cells. Beginning of December. × 400.
17. A set of four spores just formed (one is turned away from the observer) which are held together by the remnants of the mother-cell. Middle of December. × 400.
18. A young spore still attached to the remnants of the mother-cell. In the place of the primary central nucleus (which in the spores shown in Fig. 17, has already become dissolved) two new ones have been formed. × 400.
19. The same division has taken place in the two halves of the spore which is still attached to the remains of the mother-cell, × 400.
20. Remnants of the mother-cell from which the spores have escaped, × 400.
21. A septum is formed between the two nuclei dividing the spore into two halves, × 300.
22. One of the two newly formed cells has divided again by a transverse septum, × 300.
23. Outlines of the cells of a five-celled spore, × 400. On the 20th December.
24. A free spore similar to that in Fig. 7, × 400.
25. A young spore, one half of which has become divided irregularly by an oblique septum, × 300.

The originals of Figs. 18, 19, 20, 22 and 24, were taken from the same capsule as the original of Fig. 17.

PLATE VI.

Figs. 1—10. *Aneura multifida.*

FIG.

1. A delicate branch seen from above, × 10.
2. Fore-end of a growing shoot, seen from above, × 400.
3. Longitudinal section of a similar shoot. (The section has not touched the cell of the first degree.) × 300.
4. Longitudinal section of inflorescence, with a fruit-rudiment lately formed, and enclosed by a calyptra already much enlarged, × 50.
5. Very young fruit-rudiment, detached, × 300.
6. Longitudinal section of a more advanced fruit-rudiment, × 150.
7. Longitudinal section of the upper part of the fruit-rudiment at the commencement of the formation of the capsule, × 400.
8. Fruit-rudiment somewhat more advanced, enclosed by the large calyptra which is cut through longitudinally. On the left near the calyptra are two abortive archegonia. × 50.
9. Longitudinal section perpendicular to the surface through the gemmiferous portion of a shoot. In one of the epidermal cells a bud is in process of formation. A two-celled bud lies loose in another epidermal cell which has been torn. × 300.
10. Two gemmæ, one seen from the side, the other (which is about to send out a capillary shoot) seen from the front.

Figs. 11—15. *Aneura pinguis.*

11. Fore-end of a growing flat shoot seen from above, × 400.
12. Longitudinal section perpendicular to the surface of a thicker shoot. It bears the rudiment of an antheridium. × 300.
13. A similar longitudinal section not exactly through the middle of the shoot, × 300.
14. A young antheridium seen from the outside, × 300.
15. Rudiment of an archegonium seen from above, the microscope being focussed somewhat below the apex of the organ, × 300.

Figs. 16—21. *Blasia pusilla.*

16. Barren gemmiferous shoot seen from below, × 25.
17. Growing fore-end of a shoot seen from above, × 200.
18. End of a delicate shoot after the removal of the under leaves, seen from below, × 400.
19. Section perpendicular to the surface through the fore-end of a growing shoot, × 200.
20. Similar section of a shoot where the latter has a bud-receptacle in process of formation, × 200.
21. Longitudinal section of a further developed bud-receptacle, × 60.
22. Portion of a longitudinal section of a less developed bud-receptacle, upon the inner wall of which rudimentary gemmæ, in different stages of development, are seated, × 200.

FIG.

22*b*. A portion of the uppermost bud of the former figure, × 600. The dotted lines show the course of the two nuclei during the molecular motion which they exhibited.

23. Two spore-mother-cells held together by the common membrane of the mother-cell, after the formation of the tertiary nuclei, × 300.

24. A similar mother-cell somewhat more developed, × 300.

FIGS. 25—37*b*. *Fossombronia pusilla.*

25. Two-celled rudiment of a leaf, × 300.

26. A young leaf with eleven cells, × 300.

27, 28. Tips of somewhat more developed leaves, × 300.

29, 30. Sections of young archegonia, fig. 29, × 100; fig. 30, × 400.

31. Section of an archegonium in whose central cell the germinal vesicle is being formed, × 300.

32. Section of an archegonium in whose central cell the germinal vesicle is completely formed, and the primary nucleus almost dissolved, × 300.

33. Longitudinal section of an archegonium, with its central cell almost filled by the germinal vesicle, × 300.

34. Spore-mother-cell, after the formation of the four tertiary nuclei, × 300.

35. Mother-cell from the same capsule, after long soaking in water. The inner layer of the cell-membrane is much swollen, and has squeezed the confluent cell-contents into a globular lump. × 300.

36. Young elater from the same capsule after soaking in water for a short time. The middle layer of the cell-membrane is much swollen, and has ruptured the outermost one. × 300.

37. Longitudinal section of a ripe antheridium whose apex has burst by the separation of the cells and the tearing of the cuticle, × 150.

37*b*. Ruptured mother-cellule of a spermatozoon, which is escaping out of the fissure, × 600.

PLATE VII.

FIGS. 1—3. *Haplomitrium Hookeri.*

1. Longitudinal section of the apex of a leafless subterranean shoot, × 300.

2. Similar section of a similar shoot farther from the apex, × 300.

3. Similar section of a detached young fruit rudiment, × 300.

4. *Trichocolea tomentella.*—Longitudinal section of a terminal bud, × 200.

5. *Madotheca platyphylla.*—Longitudinal section of an antheridium, × 200.

6. Ripe mother-cell of a spermatozoon from the same.

FIGS. 7—9. *Ptilidium Ciliare.*

7. Half of a young leaf, × 150.

8. A young leaf slightly more developed, detached from the stem and expanded, × 200.

9. Lateral view of a terminal bud, which has developed a lateral branch close underneath the apex.

FIGS. 10—11. *Alicularia scalaris.*

FIG.

10. End of the stem being a half-ripe fruit, in a longitudinal section which has grazed the capsule and laid bare the outer surface of the fruit-stalk and of the swelling at its lower end, × 30.

11. Longitudinal section of a germ-plant, × 300.

11^{b}. A young leaf detached from the stem spread out, × 100.

12. *Jungermannia bicuspidata.*—An archegonium just impregnated, and an unimpregnated one; both laid open by a longitudinal section passing through the perianthium, which already extends far above the archegonium, and has the apices of its edges inclined towards one another. In the inner cavity of the perianthium several moving spermatozoa were found; the arrow shows the direction of their motion. × 400.

FIGS. 13—20. *Jungermannia divaricata.*

13. Longitudinal section of a rudimentary archegonium, × 600.

14. Longitudinal section of a perianthium containing only two young archegonia, × 600.

15. Archegonium ready for impregnation (or just impregnated ?), cut through longitudinally so that the knife passed through the central cell, × 600.

16. The germinal vesicle detached from the central cell of a similar archegonium. The cell-membrane has been injured by the dissecting needle; the nucleus escaped out of the fissure, and lies near it, × 500.

17. Longitudinal section of an impregnated archegonium which has grazed the two-celled fruit-rudiment. At the apex of the archegonium, between the globular lumps of glassy transparent mucilage, thread-like bodies, like spermatozoa are seen. × 600.

18. A young, and 19, a somewhat older fruit-rudiment, the former seen from the outside, the latter in longitudinal section, × 400.

20. Longitudinal section of a more developed fruit, × 250.

PLATE VIII.

FIGS. 1—20. *Jungermannia bicuspidata.*

1. A very young perianth laid open by a longitudinal section, with three archegonia still closed at the apex, × 300.

2. Longitudinal section of an archegonium ready for impregnation, × 300.

3. Similar section of a somewhat more developed perianth. In the middle is an archegonium just impregnated; near the latter are two unimpregnated ones, with ruptured apex; on the outside are two still undeveloped. × 250.

4. Four-celled fruit-rudiment detached, × 300.

5. Young fruit-rudiment. 5^{b}. The same turned round 90°. 5^{c}. A similar fruit-rudiment detached. × 300.

6. Longitudinal section of the lower part of a perianth enclosing two fruit-rudiments, × 250.

FIG.

7. Longitudinal section of a half-ripe fruit, with the calyptra, two abortive archegonia, and the lower part of the perianth, × 200.

8 and 9. Young leaves which have not yet formed the rudiments of the two tips, × 500.

10. A further-developed leaf, × 500.

11. Tip of a half-developed leaf, × 300.

12. Section of the tip of a leafless subterranean shoot; 12^b, section of the same shoot after being turned round 90°. × 300.

PLATE IX.

FIGS. 1.—12. *Jungermannia bicuspidata.*

1. Ripe spore, × 300.

2—10. Different stages of germination. 2, 3 one week. 4, 5 three weeks. 6, 7 four weeks after sowing. 8—10, germ-plants a year old. 2—6, × 300; 7, × 200; 8, 9, 10, × 100; 10^b is the upper end of fig. 10; turned round 90° and × 400.

11. Fore-end of a germ-plant at the stage of development shown in fig. 8, seen from the outside. The boundaries of the cell of the first degree, and of the first cell of the second degree, as they appear in an optical section, are shown by dotted lines, as is done also in the following figures. × 400.

11^b. The same. The apex of the stem turned round 90°.

11^c. The same, turned round 270°.

11^d. The apex of the stem of a more-developed germ-plant, in a position intermediate between that of figures 11 and 11^b, seen from the outside, × 400.

12. An abnormal pro-embryo, in which the rudiment of the first leaf-bearing axis does not proceed from one of the apical cells of the pro-embryo, but springs from a point lower down (five months after sowing), × 200.

12^b. Rudiment of the leafy axis, turned round 90°.

FIGS. 13—16. *Lophocolea bidentata.*

13. Longitudinal section of a terminal bud, × 600.

14. A very young, 15 a somewhat older leaf seen from above, × 600.

16. A more developed leaf, the two halves of which have developed unequally, × 300.

FIGS. 17—30. *Lophocolea heterophylla.*

17—25. Germination of the spores; (17, a spore just detached, 18 a spore twenty-four hours afterwards), × 200 except fig. 23, which is × 600.

26. Production of the first leafy axis out of the pro-embryo, × 250.

27. More advanced germ-plant, whose hinder end is already dead, × 200.

28. Lower portion of a germ-plant which has already formed some perfect leaves, × 100.

FIG.
29. Portion of the stem of a young plant, lateral view of the outer surface. The inner edges of contact of the cells are shown by dotted lines. × 150.
30. Longitudinal section of the upper end of a young archegonium, × 200.

FIGS. 31, 32. *Jungermannia intermedia.*

31. Longitudinal section of a half-ripe antheridium, × 300.
32. Similar section of a young fruit-rudiment of the same plant, × 300.

FIGS. 33, 34. *Jungermannia trichophylla.*

33. Longitudinal section of a young fruit, × 200.
34. A set of special-mother-cells out of the same fruit, × 600.

PLATE X.

CALYPOGEIA TRICHOMANES.

1 and 6. Longitudinal sections of young fruit-branches, × 200.
2, 4, 5. Detached fruit-rudiments seen from the outside, figs. 2 and 4, × 300, fig. 5, × 150.
3, 7. Longitudinal sections of similar fruit-rudiments, × 300.
8. Longitudinal section of the lower part of a young fruit-sac, × 200.

PLATE XI.

FIGS. 1—7 and 15—26. *Radula complanata.*

1. Lateral view of an inflorescence; the antheridia and archegonia are represented in section; the cell contents are not shown.
2. A very young, 3 a half-ripe antheridium, both in longitudinal section, × 500.
4. Longitudinal section of a more developed fruit-rudiment, together with the lower part of the surrounding calyptra, × 200.
5. Longitudinal section of a young fruit-rudiment, × 500.
6. Longitudinal section of a somewhat dwarfish fruit-rudiment at the commencement of the differentiation of the capsule-wall and contents, × 300.
7. Lower end of the stalk of a half-ripe fruit, × 200.
15. Two lobes of a somewhat developed leaf spread out, × 200.
16. Ripe spore, × 200.
17—24. Different states of the development of the flat pro-embryo, 20, 21, and 22 are lateral views, × 200.
25[a]. The terminal bud of the first leafy axis, × 300.
25[b], 26. The first leafy axis proceeding from the pro-embryo, × 300.

FIGS. 8—14, 27—42. *Frullania dilatata.*

FIG.

8^{a}, ^{b}, ^{c}. Three successive stages of development of superior leaves. In fig. 8^{c} the under lobe of the leaf is shown as a single row of cells. 8^{a} and 8^{b} are × 300, 8^{c} is × 150.

9. Leaf bud seen from above, × 200.

10. Leaf bud seen from the upper side, × 200.

11. A young inferior leaf, × 300.

12. Two lobes of a young superior leaf spread out, × 200.

13, 14. Upper lobes of older superior leaves, × 200.

27. Ripe spore just set free, × 300.

28, 29. Spores at the beginning of germination, having become bicellular, × 300.

30—36. Outlines of the cells of germinating spores; in figs. 30—33 the outer spore-membrane is shown; 36^{b} is the germ-plant shown in fig. 36 turned round 90°.

37, 38. Germ-plants more developed seen from the outside.

39. A very young, 40 a more developed, 41 a half-ripe, 42 a ripe ruptured antheridium; near the latter are some escaped mother-cells of spermatozoa, from some of which the spermatoza have already escaped, × 400.

PLATE XII.

FRULLANIA DILATATA.

1. Two young archegonia surrounded by the rudiment of the perianth, × 400.

2. Longitudinal section of a perianth seen from the outside, × 400.

3. Longitudinal section of an inflorescence containing two half developed and one impregnated archegonium, × 400.

4. Longitudinal section of the lower part of an impregnated archegonium, with a seven-celled fruit-rudiment, × 400.

5. Longitudinal section of a more developed fruit-rudiment, with the archegonium becoming transformed into the calyptra, × 400.

6, 7. Young fruit-rudiments, detached. 6 and 6^{b}, 7 and 7$_{b}$, are the same preparations, 6 and 7 being the figures obtained by adjusting the microscope to the longitudinal axis, and 6^{b} and 7$_{b}$ by adjusting it to the outer surface, × 400.

8. Longitudinal section of a more developed fruit, at the time of the differentiation of the capsule-wall and contents, × 300.

9. Longitudinal section of a half-ripe fruit, × 300.

10. Spore-mother-cell with four protrusions (one turned away from the observer) of the membrane, taken from a similarly developed capsule, × 300.

PLATE XIII.

RICCIA GLAUCA.

FIG.

1. Germ-plant (from a shady habitat) to which the spore is still attached, × 200.
2. Developed germ-plants from the same locality, × 20.
3. Perfect shoot seen from below, × 8.
4. A young shoot in the bud seen from above, × 30.

4ᵇ. Fragment of a capillary root of the median line of a perfect shoot. The inner wall is furnished with prominent points, × 200.

5. Three-celled rudiment of antheridium not yet grown over by an annular wall, × 200.
6. Rudiment of an antheridium and part of a longitudinal section of a very young shoot. The yet undivided mother-cell of the organ is already grown over by an annular wall. × 300.

7ᵃ. Longitudinal section through the fissure of the fore-edge of a perfect shoot. The upper part of the figure is the lateral surface—through which the section has passed—of the deep indentation of the fore-edge; the shaded part is the cavity of the lower portion of the latter, in which the median shoot is developed. × 30.

7ᵇ. Longitudinal section of the median shoot bearing two rudiments of antheridia, one is unicellular and the other is a few-celled oval body surrounded by a wall closing over the apex of the organ, × 400.

8. Longitudinal section of a half-developed antheridium, × 300.
9. Similar section of an almost ripe antheridium, × 200.
10. Mouth of the sheath of a ripe antheridium, seen from the outside, × 300.
11. Longitudinal section of a young shoot bearing the rudiment of an archegonium, × 400.
12. Section of a more developed rudiment of an archegonium, × 400.
13. Section of an archegonium whose longitudinal growth is terminating, × 300.
14. Longitudinal section of a shoot bearing an archegonium ready for impregnation, × 300.
15. An abortive archegonium whose mouth has been laid open by a longitudinal section through the shoot, × 300.
16. Section of an impregnated archegonium with a fruit-rudiment still unicellular.

16ᵇ. Lower part of a section of an archegonium lately impregnated with a three-celled fruit-rudiment, × 200.

17, 18. Longitudinal sections of an archegonium with more fully developed fruit-rudiments, × 300.

19. Longitudinal section of a young capsule enclosed by the calyptra, × 200.

PLATE XIV.

RIELLA REUTERI.—*Mont.*

FIG.

1 and 2. Germ-plants with spore attached, × 150.

3. A plant produced by the multiplication of a cell of a leaf separated mechanically from an older individual, × 130.

4. Adventitious shoot of an older plant, × 150.

5. Full-grown shoots (cultivated, more slender than in the natural state); the older part of the plant is dead, × 5.

6. Another similar shoot, × 20.

7[a]. The end of the shoot *a* of the latter, × 200.

8. Terminal bud of a strong shoot after the removal of the older leaves, × 200. The leaves and the upper layer of cells of the massive portion of the stem—which latter, as far as the drawing extends, consists of only two layers of cells—are shown in dark lines above the outlines of the membranous wing and the second cellular layer of the stem.

9. Longitudinal section of a terminal bud perpendicular to the surface of the stem, × 200.

10. Terminal bud after the removal of all leaves. Two antheridia are being formed, the one sunk half down, the other deep down into the duplications of the margin of the wing, × 150.

10. Young unicellular antheridium with adjoining tissue, laid bare by a section parallel to the surface of the wing of the stem, × 150.

12. Longitudinal section of a half-ripe antheridium, × 150.

13. Section through a portion of a fertile shoot which has laid bare an archegonium recently impregnated, and has grazed a lateral axis bearing antheridia, × 100.

14[a]. Unimpregnated archegonium with its apex still closed, × 250.

14[b]. Archegonium ready for impregnation, × 250.

15. Longitudinal section of a recently impregnated archegonium, × 250.

16. Young calyptra just visible through its veil, × 25.

17. Longitudinal section of a calyptra with sporangium (a younger state than Fig. 16), × 200.

18. Longitudinal section of the same when half ripe, the section not having passed through the mouth, × 100.

19[a]. Mother-cell with four spores enclosed in special-mother-cells, × 250.

19[b]. Rudimentary elater from the same sporangium, × 250.

PLATE XV.

FIGS. 1—18. *Marchantia polymorpha.*

1. Longitudinal section perpendicular to the surface of a shoot bearing a very young bud-receptacle, × 50.

1[b]. The bud-receptacle of the last figure cut through, × 200.

2. Young bud, × 400.

FIG.

3, 4. Longitudinal moieties of more developed buds, seen from the surface, × 300.

5. Half of the fore-edge of a more advanced bulbil, × 300.

7. Bud, whose upper part is beginning to widen, seen from the surface, × 50.

8. The cells of an indentation of a lateral margin of the latter bud, × 300.

9. Bud which has rooted and is beginning to sprout, × 15.

10. Longitudinal section through a shoot bearing the rudiment of a fruit (beginning of April), × 50.

11. Head of young fruit from below (end of May), × 100.

12. More advanced fruit in longitudinal section, × 100.

13, 14. Longitudinal section of impregnated archegonia, × 300.

15. Impregnated archegonium, enclosing a four-celled fruit-rudiment, and which together with its special covering has been laid open by a longitudinal section grazing the fruit-rudiment.

16. Margin of a growing disk of antheridia (end of November) in longitudinal section, × 300.

17. Transverse section of the stem of a developed antheridial disk, × 100.

FIGS. 18—20. *Lunularia vulgaris.*

18. Longitudinal section perpendicular to the surface, of a very young shoot, × 300.

19. Similar section of the end of a young shoot bearing the rudiment of a bud-receptacle.

20. End of a shoot, × 5.

FIGS. 21—28. *Targionia hypophylla.*

21. Longitudinal section, perpendicular to the surface, through a shoot whose fore-end bears archegonia, enclosed by the rudiment of the veil, × 100.

22. Similar section of a recently impregnated archegonium, × 300.

23. Longitudinal section of an archegonium enclosing a multi-cellular fruit-rudiment, × 300.

24. Young fruit-rudiment detached, 24^b is the same turned 90° round its longitudinal axis, × 300.

25. Longitudinal section of a more developed fruit-rudiment detached, × 500.

26. Similar section of a more developed fruit-rudiment, × 300.

27. Spore-mother-cell still exhibiting its primary nucleus, × 400.

28. Spore-mother-cell in which the four secondary nuclei have been produced, and having projecting ridges upon the inner surface of the cell-membrane, × 400.

29. Young elater from the same fruit as that which produced the mother-cell shown in fig. 27, × 400.

30. Young elater from the fruit which produced the spore-mother-cell shown in fig. 28, × 400.

PLATE XVI.

FIGS. 1—13. *Fegatella conica.*

FIG.

1. Section parallel to the surface of a shoot formed in autumn and destined for development in the following spring, × 30.
2. One of the side shoots of this shoot, × 300.
3. Longitudinal section perpendicular to the surface of a similar young shoot, × 300.
4. Stomata, in process of development, × 300.
5. Rudiment of a fruit-head (beginning of February), in longitudinal section, × 300.
6. Young fruit-head from below, × 100.
7. Fruit-head at that stage of development when the archegonia are ready for impregnation, × 50.
8. Young fruit-rudiment with the calyptra enclosing it, and the adjoining portions of the fruit-head, in longitudinal section, × 200.
9. Five-celled fruit rudiment, detached, × 400.
10. More developed fruit rudiment in longitudinal section, × 300.
11, 12. 11 a very young, 12 a somewhat more developed leaf, × 300.
13. Outline of a half-developed leaf, × 30.

FIGS. 14—20. *Rebouillia hemispherica.*

14. Longitudinal section perpendicular to the surface through the very young rudiment of a shoot. × 300.
15. Outer aspect of the same preparation, after it has been laid upon the sectional surface passing through the longitudinal axis of the shoot. The rudiments of two leaves are seen. × 300.
16. A young leaf, × 300.
17. Longitudinal section perpendicular to the surface of a fertile shoot. On the right is a fruit-head; the section has passed through two unimpregnated archegonia and four scales. Stomate-formation is just commencing in the covering cells of the air-cavities of the fruit-head. Further back is a cushion of antheridia, cut through. The outlines of the cells only are drawn, and the contents of the antheridia omitted. × 300.
18. An impregnated archegonium in longitudinal section. The mother-cell of the fruit-rudiment is still undivided. × 300.
19. Longitudinal section of an impregnated archegonium, enclosing a more developed fruit-rudiment. One only of the rows of cells of which the young fruit-rudiment consists is seen; the position of the nuclei of the second is shown by a dotted circle. × 300.
20. One of the sheathing prolongations of the fruit-head which enclose the fruit, seen from below. The curved neck of the impregnated archegonium is also seen. × 30.

PLATE XVII.

FIGS. 1—8. *Sphagnum cymbifolium.*

FIG.

1. Longitudinal section of the terminal bud of the median shoot of a full-grown plant. The section has passed underneath the fifth leaf of the left side of a lateral shoot. × 150.
2. Longitudinal section of a young innovation, × 600.
3. Terminal bud of a median shoot, detached and seen from the outside, × 600.
4. Terminal bud of a median shoot with left-handed $\frac{2}{5}$ phyllotaxis, seen from above, × 500.
5. Terminal bud of a median shoot, detached by two transverse sections, of which one passed close down the apical point of the transverse cell, the other through the stem close underneath the third-youngest leaf. All the older leaves are cut through transversely. The leaves from α to β have a right-handed $\frac{2}{5}$ arrangement; from thence upwards the arrangement is $\frac{3}{8}$ and left-handed. × 500.

5^b. Diagram.

6. Young lateral bud, seen from the outside, × 500.
7. Longitudinal section of a part of an innovation, taken at the point where the growth in thickness of the stem ends, × 500.
8. Longitudinal section of one of the longitudinal moieties of a somewhat lower part of the same innovation, × 200.
9. *Sphagnum acutifolium.*—Fragment of a longitudinal section of the circumference of the stem of the principal shoot from the lower boundary of the region where lateral shoots are crowded together. The cells of the interior of the stem have pitted walls. × 200.

9^b. One of these pitted cells, × 600.

PLATE XVIII.

1. A young leaf of Sphagnum acutifolium, seen from the surface, × 400.
2. Fragment of a somewhat more developed leaf of the same species, in whose cells the third division is beginning, × 400.
3. Fragment of a leaf of Sphagnum cymbifolium in which the cells with, and those without chlorophyll are entirely differentiated. Several of the former have divided by transverse septa, × 400.
4. Fragment of a leaf of Sphagnum acutifolium in whose cells, which are devoid of chlorophyll, the formation of annular and spiral vessels has commenced. Several of the latter cells have divided by longitudinal or transverse septa. × 400.

FIGS. 5—13. *Sphagnum acutifolium.*

5. Pro-embryo which has not yet developed any leafy shoots, × 10.
6. A very young pro-embryo, × 200.

FIG.

7. An unusually small pro-embryo; on the left, near the lower angle, the bud of a leafy shoot is seen. A new pro-embryo has originated at one of the rows of cells springing from the marginal cells. × 100.

8. Basal fragment of a highly developed pro-embryo to which the spore is still attached. The smaller longitudinal moiety of the leafy bud, which is seated very near the cell, has been removed by the section. × 200.

9. Lobe of a pro-embryo, without any processes from the marginal cells, with a bud attached, × 100.

11, 12. 11 a very young, 12 a half ripe antheridium, in longitudinal section, × 300.

13. Ripe spermatozoa, killed by iodine, × 800.

FIGS. 14—17. *Sphagnum cymbifolium.*

14, 15. 14 a very young archegonium, 15 archegonium near the period of opening; in longitudinal section, × 250.

16, 17. Longitudinal sections of the ends of stems in which the rudimentary cells of a lateral branch have been exposed by the section (see the left side of both figures; in fig. 16 underneath the uppermost, in fig. 17 underneath the second uppermost leaf). × 150.

18. *Schistostega osmundacea.*—Portion of a pro-embryo, × 300.

PLATE XIX.

FIGS. 1—16. *Funaria hygrometrica.*

1—4. Sections of antheridia in different stages of development, × 300.

5—8. Mouths of unimpregnated archegonia. 6 and 7 the central cell, × 300. Figures 5 and 6 are young states, figures 7 and 8 more developed conditions.

9. Young fruit-rudiment in longitudinal section, × 300.

10. The upper end of the same, × 300.

11. Upper part of a growing calyptra, with the upper half of the enclosed fruit-rudiment: in longitudinal section. The fruit-rudiment which has not been cut through is shown in an optical longitudinal section. × 300.

11^{b}. The fruit-rudiment out of the same calyptra, detached, turned round 90°, and in longitudinal section, × 300.

13. Spore-mother-cell after the formation of the two secondary nuclei, × 400.

14. The same; after the formation of the four tertiary neuclei, × 400.

15. The same; after the divisions of its internal cavity into four special mother-cells, × 400.

16. The same; after considerable thickening of the walls of the special-mother-cells and the formation of the spore-membrane, × 400.

17. Longitudinal section of the upper half of the mouth of a recently impregnated archegonium of *Dicranum heteromallum.* Underneath is the primary cell of the fruit-rudiment detached from the central cell of the archegonium by contact with the dissecting needle. × 300.

18. *Bryum cæspiticium.*—Rudiment of a lateral bud, detached and seen obliquely from above, × 300.

FIG.

19. *Racomitrium ericoides.*—Fragment of a lateral branch of a pro-embryo with the attached germ-plant, × 300.

20, 21. *Fissidens bryoides.*—Longitudinal sections of archegonia, fig. 20 ready for impregnation, fig. 21 just impregnated, × 300.

22. Young fruit-rudiment of *Bryum argenteum* detached, × 300.

22^{b}. The same turned round 90°, × 300.

23. Longitudinal section of the vaginula, and of a fragment of the seta, and the adjoining parts of the shoot of the same species, × 25.

PLATE XX.

PHASCUM CUSPIDATUM.

1. Longitudinal section of a rudiment of an archegonium, × 400.
2. Similar section of a young archegonium, × 400.
3. Upper end of the same, × 600.
4. Longitudinal section of an archegonium, whose apical cell has ceased to multiply, × 250.
5. Longitudinal section of an archegonium shortly before the rupture of the apex, × 500.
6. Archegonium whose apex has lately burst, in longitudinal section. The still globular daughter-cell within the central cell only fills a small portion of the latter, × 250.
7. Accidental transverse section of the place of junction of the neck, and the ventral portions of an archegonium, × 250.
8. Central cell of the ventral portion of an archegonium which has been cut longitudinally, in the state of development shown in fig. 6, × 500.
9. Archegonium just impregnated, × 400.
10. Longitudinal sections of the lower part of the neck, and of the upper part of the ventral portion, of an archegonium, with a two-celled fruit-rudiment uninjured by the section, × 300.
11. Similar section of an archegonium with a four-celled fruit-rudiment, × 200.

11^{b}. A fruit-rudiment, detached, × 400.

11^{c}. Perspective view of the course of the cell walls of the same.

12^{a}. A four-celled fruit-rudiment, detached, × 400.

12^{b}. The same turned round 90°.

13. Longitudinal sections of an impregnated and abortive archegonium, × 300.
14. Similar section of a detached fruit-rudiment, × 200.
15. Similar section of a fruit-rudiment with the growing calyptra and vaginula, × 75.

15^{b}. Outside of the apex of the same fruit-rudiment, × 400.

16. Portion of the contents of an almost ripe antheridium. Each of the polygonal cellules of the interior of the organ encloses the mother-cell of a spermatozoon. × 600.

PLATE XXI.

FIG.

1. Longitudinal section of a fruit-rudiment, × 200.

2ª. Section of the apex of a less advanced fruit-rudiment, × 250.

2ᵇ. The same turned round 90°, × 250.

3. A younger fruit-rudiment whose lower part is very highly developed, seen from the outside, × 30.

3ᵇ. Upper part of the same in longitudinal section, × 250.

4. Longitudinal section of calyptra; the outer side of the spindle-shaped fruit-rudiment is seen. × 60.

5. Longitudinal section of a young fruit, × 200.

6. A portion of the layer of mother-cells and of the adjoining tissue of a fruit at a similar stage of development. The primordial utricles of the mother-cells are contracted by having lain in water for a quarter of an hour. × 500.

7. Section at right angles to the longitudinal axis of a fruit, passing through a larger portion of the layer of mother-cells, × 150.

8. A spore-mother-cell out of whose bursting membrane the globular distended primordial utricle is emerging, × 300.

9. Primary mother-cell from the transverse section of a young capsule. The cell-contents are beginning to become contracted and constricted, indicating the commencement of the formation of the spore-mother-cells. × 250.

PLATE XXII.

1. Spore-mother-cell whose primordial utricle only partly fills the cavity and is lying against the wall, × 500.

2. Two primary mother-cells of the second degree, formed by the division of of a primary mother-cell of the first degree by means of a septum parallel to the longitudinal axis of the fruit. Each exhibits only one of the longish ellipsoidal spore-mother-cells enclosed within. One of the latter cells is beginning to divide. The section is at right angles to the longitudinal axis of the fruit. × 300.

3. Primary mother-cells, each with two free globular spore-mother-cells, in which division is about to commence. Direction of the section as in the last figure. × 300.

4. Longitudinal section through some primary mother-cells of a somewhat more developed fruit, × 200.

5. Young spore from the same, × 500.

FIGS. 6—21. *Gymnostomum pyriforme.*

6. Longitudinal section through the upper end of a fruit-rudiment whose apical cell has ceased to multiply in the direction of its length, and whose expansion in breadth underneath the apex is just beginning. The top of the specimen was destroyed by the section; the representation of the boundaries of the cells at that part is shown hypothetically by dotted lines. × 400.

FIG.

7. Longitudinal section of a very young fruit, whose apophysis is far larger than the capsule, × 60.
8. A portion of the layer of mother-cells and of the adjoining tissue of a similar fruit cut through longitudinally, × 300.
9. A similar preparation from a somewhat more developed theca. The contents of the primary mother-cells of the spores and of the adjoining cells of the columella are also shown. The primordial utricles of the latter have contracted by lying in water. × 300.
10. A similar preparation from a more advanced capsule, × 300. Here the nuclei of the cells immediately adjoining the layer of spore-mother-cells, *i. e.*, of the so-called inner capsule-wall, and the arrangement of the chlorophyll of the outermost cells of the same are shown. The chlorophyll in these cells lies closely attached to the free outer wall.
11. Similar preparation from a capsule in which the formation of the spore-mother-cells within the primary mother-cells is just about to take place, × 300.

12, 12^a. Spore-mother-cells with the enveloping primary mother-cells, × 300.

13—21. Stages of development of the spore-mother-cell, × 600.

13. Young spore-mother-cell with central nucleus and homogeneous granular mucilaginous fluid contents.
14. The nucleus is pushed near to the wall; the protoplasm is accumulated chiefly in the middle point of the cell.
15. This accumulation has divided into two halves.
16. A secondary nucleus appears in each of them.
17, 18. Four tertiary nuclei are seen in the place of the two secondary nuclei.
19. The primary nucleus of the mother-cell has disappeared.
20, 21. Spores fully formed.

PLATE XXIII.

FIGS. 1—11. *Archidium phascoides.*

1. Archegonium ready for impregnation, × 250.
2. Archegonium just impregnated, × 400.
3. Fruit with two archegonia which have been some time impregnated, in longitudinal section, × 200.
4. A young calyptra just ruptured by the swelling fruit, opened laterally, × 300.
5. Young fruit cut through longitudinally and detached, × 200.
6. The same somewhat more developed. The primary mother-cell of the spores has fallen out, × 200.
7. The same, with the full number of cells. In the interior is a primary mother-cell enclosing four mother-cells. The contents of the latter are omitted in the drawing, × 300.
8. Primary mother-cell, with four mother-cells. The contents of the special mother-cells have contracted.
9. Mother-cell with four lately formed spores, × 300.

FIG.

10. Mother-cell with four spores. The membrane of the former is beginning to dissolve, × 300.

11. Longitudinal section of ripe fruit, × 100.

Figs. 12—15. *Fissidens taxifolius.*

12. Young leaf seen from the surface, × 300.

13—15. Cells of a somewhat more developed leaf of the same species, showing different stages of development of the chlorophyll-granules, × 400.

PLATE XXIV.

1. Germinating spore of *Platycerium alcicorne.* The inner spore membrane has emerged from the ruptured exosporium in the form of a row of three chlorophyll-bearing cells. The lowest of these cells has already developed a capillary root. × 400.

2. Young prothallium of *Gymnogramma calomelanos*, × 25.

3. Young prothallium of *Asplenium septentrionale*, × 50.

4. A shoot spontaneously detached from an old luxuriant prothallium of *Gymnogramma calomelanos.* It has developed a number of antheridia, × 150.

5. End of the shoot of an old prothallium of the same species, × 2.

Figs. 6—12, *Pteris serrulata.*

6. Fore-edge of a developed prothallium, × 150.

7. Longitudinal section perpendicular to the surface, of a fully developed prothallium. The small papillæ below are antheridia, the longer ones archegonia. × 75.

8. Longitudinal section of a young antheridium, × 400.

9. Apical aspect of the same. The course of the septa of the central cell is shown by dotted lines. × 400.

10. Same view of a more developed antheridium, whose central cell is already divided into sixteen cells, × 400.

11. Side view of an almost ripe antheridium, × 300.

12. Same view of an empty antheridium, × 400.

13, 14, 15. Spermatozoa of *Asplenium septentrionale*, killed with iodine. 13 is × 1200, 14 and 15 are × 300. 13 and 14 are lateral views, and 15 is seen from above. The mother-cell is still attached to the spermatozoon in fig. 14.

Figs. 16—19. *Ceratopteris thalictroides.*

16. Young prothallium with attached spore, and an antheridium, × 150.

17—19. Lateral views of young antheridia, × 300.

PLATE XXV.

FIG.

1. *Aspidium filix-mas.*—Longitudinal section of a young archegonium in process of formation, × 200.
2. *Gymnogramma calomelanos.*—Similar section of a slightly more developed antheridium, × 400.
3. *Pteris serrulata.*—Archegonium soon after the formation of the germinal vesicle, × 400.
4. An archegonium of the same fern without the axile cellular row of the neck, at the same stage of development, × 400.
5. *Aspidium filix-mas.*—Longitudinal section of a similarly developed archegonium, × 200.
6. *Gymnogramma calomelanos.*—Transverse section of the neck of an archegonium at the same stage of development, × 200.
7. Further developed archegonium of the same fern shortly before the bursting of the apex, in longitudinal section, × 400.
8. *Pteris serrulata.*—A similarly developed archegonium, × 400.
9. Central cell of an archegonium of the same fern, it has been grazed by a longitudinal section, and the germinal vesicle thereby injured, so that it exhibits folds of the membrane, × 500.
10. Central cell of an archegonium of the same fern seen from above. The microscope has been focussed to the upper surface of the cell of one of the first archegonia of a young prothallium, whose parenchymatal cushion was still thin, and permitted the passage of much light. × 400.
11. *Pteris serrulata.*—Portion of a longitudinal section of a prothallium with two archegonia; one with the apex just burst, the other nearly ready to burst, × 400.

PLATE XXVI.

1. *Gymnogramma calomelanos.*—End of a shoot of a prothallium, × 5.
2. *Gymnogramma chrysophylla.*—Abnormal archegonium, from a longitudinal section of an old luxuriant prothallium, × 200.
3. *Gymnogramma calomelanos.*—Portion of a longitudinal section of an old luxuriant prothallium, which has a knob-like excrescence, × 50.

3b. Cortical layer and some of the cells of the inner tissue—filled with a mass of mucilage and oil—of the above knob, × 300.

FIGS. 4—20. *Aspidium filix-mas.*

4. Archegonium at the moment of impregnation. In the central cell of the archegonium—which has been grazed by two longitudinal sections—are three spermatoza still in motion. The inner mouth of the canal of the neck has already become closed again by the expansion of the surrounding cells. × 300.
5. Longitudinal section of an archegonium shortly after impregnation. The enlarged impregnated germinal vesicle does not yet quite fill the central cell. × 300.

FIG.

6. Longitudinal section of the fragment of a prothallium, showing an impregnated archegonium with a multi-cellular embryo which has been grazed by the section.

6^b. The net of cells of this embryo; the boundaries of the cells are drawn of different thicknesses, according to their age.

7, 7^b. More advanced states of 6 and 6^b.

8. The end of the first frond of a more developed embryo, seen from the surface, × 300.

9, 10, 11. Transverse sections through the stipes of a frond of a one-year-old seedling—9, at the base; 10, somewhat higher up; 11, still higher. × 20.

12, 16, 17. Transverse sections through the stem of a one-year-old seedling. 12, at the base; 16, in the middle; 17, near the top. × 30.

13. Germ-plants after the development of the frond, in longitudinal section. Between the first and second root of the primary axis of the embryo. × 20.

14. The top of the stem of a seedling of ten months old, seen from above. On the left is the rudiment of the youngest and on the right that of the next oldest frond. The roundish cells, with granular contents, are either mother-cells, or cells of attachment, of scales. × 200.

15. A ten-months old seedling, in longitudinal section. The protuberance below on the left is the primary axis of the embryo. × 20.

18. Basal outline of a young frond of a seedling, and of the scales surrounding it, × 30.

19. Upper part of the stem of a full-grown plant cut through longitudinally. The cellular tissue—up to the vascular bundles—of the divided frond is removed, to show the course of the bundles. Natural size.

20. A mesh of the net of vascular bundles of a similar stem, with the stumps of the vascular bundles passing from it to the fronds. × 5.

PLATE XXVII.

1, 2. Apical views of the ends of the stem of full-grown plants. Fig. 1 with a right-handed, fig. 2 with a left-handed, cell-succession. × 200.

3, 4. Longitudinal sections of terminal buds of full-grown plants. Fig. 3 × 200, fig. 4 × 170. In fig. 4, *w* represents the rudiment of a frond divided by the section.

5. A frond still rolled up, the scales having been removed, seen from the back, showing the rudiment of an adventitious bud. Natural size.

6. Lower part of a stipes, whose lamina is already dead; with an adventitious bud in process of development. Natural size.

7. The same object, laid bare up to the vascular bundles of the cortical tissue. Natural size.

8. Longitudinal section of the tip of a root, × 200.

9. Transverse section of the same, passing through the punctum vegetationis at the height *a b* of the previous figure, × 300.

10. The middle region of a similar section, somewhat lower down, at the position *c d* of the root in fig. 8, × 300.

PLATE XXVIII.

Figs. 1—6. *Pteris aquilina.*

FIG.

1. Archegonium, with the adjoining cells of the prothallium, in longitudinal section. The embryo consists of four cells lying in the plane of the section. × 300.
2. Longitudinal section of the fore part of the cushion of a prothallium, which, besides the impregnated archegonium laid bare by the section, and whose central cell is not quite filled by the rudimentary embryo, bore a second impregnated archegonium with a far more developed embryo. Above the cushion of cellular tissue there is seen a portion of the membranous wing of the prothallium, which has been cut by the section. × 150.
3. An unimpregnated archegonium, and one which has been some time impregnated, in a longitudinal section of one and the same prothallium. × 300.

3ª. The cellular net of the embryo of the latter figure. The lines which answer to the boundaries of the cells of the older generation are much thickened. The group of cells *a-c* is the rudiment of the principal bud, and of the first frond; the group *a-d* is the rudiment of the root.

4. A similar preparation from a more developed prothallium. The cells of the first degree of the root are here very visible. × 300.
5. Longitudinal section through the cushion of cellular tissue of a prothallium. The section has passed through an archegonium with a far more developed embryo. × 300.

Figs. 7—8. *Pteris serrulata.*

7. Optical transverse section of the central cell of an archegonium just impregnated. The germinal vesicle contains two nuclei. × 300.
8. Longitudinal section of a prothallium, with an embryo in the state of development of that of *Pteris aquilina*, as shown in fig. 5. × 35.

PLATE XXIX.

PTERIS AQUILINA.

1. Longitudinal section of a young plant which has recently broken through the archegonium. A portion of the prothallium to which it is attached is figured. × 150.
2. Imaginary outline of a more developed germ-plant—B the primary axis, A the first, D the second frond; between the two the position of the apical cell is indicated; C the first, E the second, F the third adventitious root.
3. The fore-edge of the first frond of a germ-plant in the same state of development, seen from the fore-surface, × 100.

FIG.

4. Longitudinal section of the end of the bud of the principal axis of the same, × 400.
5. A further developed germ-plant shown in a longitudinal section through the median lines of the first two fronds. The first and fourth adventitious roots have been cut by the section.
6. A more developed germ-plant shown in a longitudinal section at right angles to the former one, the section passing through the second and third adventitious root.
7. Transverse section of the older portion of the axis of a seedling of a month old, × 30.
8, 9. Transverse section of the same nearer the apex.
9^b. The same at another neighbouring point of the same axis, × 5.
10, 11. Seedling of a year old. Natural size.
12, 13. Transverse section of the stem of the same, taken near the apex, × 5.
14. Transverse section of the third frond of a germ-plant, × 10.
15. The end of a vigorous shoot in November. Natural size. Adjoining the end of the stem is seen the frond destined for development in the following spring. More to the left is seen the lower part of the frond of the current year, whose lamina has already opened.
16. Forking stem-end, seen in a section through the longitudinal ridges. The sheath of vascular bundles of the middle of the stem is laid bare by the section. Twice the natural size.

PLATE XXX.

PTERIS AQUILINA.

1, $^{a, b, c}$. A similar shoot in the spring, peeled as far as the cortical vascular bundle, in order to show its course. Seen from the left, from the right, and from above. Natural size.
1, $^{d, e}$. The principal vascular bundles of the shoot, with their ramifications to the frond of the previous year.
2. Transverse section of a stem at the place of insertion of a frond. Natural size.
3. Transverse section of a stem, × 3.
4. Longitudinal section of the terminal portion of the apex of a frondless stem of a very old plant, × 15.
5. Apex of a stem bearing a young frond, with the rudiment of an adventitious bud, seen from above. Natural size.
6. Frond destined for development in the following year, as it appears late in autumn, after the removal of the scales; seen in front. Natural size.
6^a. The rudiment of the lamina of this frond, × 15.
7, 8, 9. Transverse sections of a stipes—fig. 7 close to the stem, figs. 8 and 9 somewhat higher up, × 3.
10. Transverse section of a portion of the lower principal vascular bundle of the stem-bud, one and a half line backwards from the apex, × 150.

FIG.

10[b]. Transverse section of the same portion of the same vascular bundle, one line and a half further back. The number of the cells has considerably diminished during the thickening of the walls of those which remain. × 150. The vessels are figured as they appear under a moderate magnifying power, the sections not being very thin.

11. Two vessels and the neighbouring cells of a complete vascular bundle seen in a very delicate transverse section, × 500.

12. Longitudinal section of the margin of a principal vascular bundle, at the place where the thickening layers begin to appear in the spiral vessels, × 500.

PLATE XXXI.

PTERIS AQUILINA.

1. Similar longitudinal section of a more advanced vascular bundle, in which the thickening layers of the scalariform vessels are seen, × 200.

2. Apex of the stem seen from above, × 300.

3. Apical aspect of the apical region of the stem exposed by a transverse section passing through the surrounding cortical substance, which has the form of a circular wall. The radiating light spots indicate the course of the cortical vascular bundles which converge towards the punctum vegetationis. × 30.

3[b]. The apical surface of this end of the stem. The apical cell is seen in the middle; on the left hand, near (and above) it is the rudiment of the youngest frond. × 300.

4. Longitudinal section, perpendicular to the horizon of the end of the stem, × 300.

5. The same in a longitudinal section parallel to the horizon, × 200.

6. Horizontal section of the end of a stem which has passed transversely through several rudimentary roots; that shown by the letter *a* is exactly in the punctum vegetationis. × 5.

6[b]. The above rudimentary roots, × 200.

PLATE XXXII.

FIGS. 1—3. *Pteris aquilina.*

1. Longitudinal section of the end of a stem. At the vascular bundle, to the left, is the rudiment of a root laid bare, for its whole length. × 15.

1[b]. The rudiment of a root just mentioned, × 300.

2. Longitudinal section of the very young frond of a seedling one year and a half old. Above the scale is the rudiment of a bud. × 250.

3. Longitudinal section of a one-year-old frond of a full-grown plant. A dormant adventitious bud is laid bare. × 10.

3[b]. The adventitious bud, × 200.

FIG.

4. Apical view of the terminal bud of *Aspidium spinulosum*, surrounded by the rudiments of the youngest fronds, × 250.

5. Diagrammatic representation of three divisions of the apical-cell of *Aspidium filix-mas* or *spinulosum*, and of the displacement caused by the change of form of the apical-cell (see p. 239). The original position of the older walls is shown by dotted lines, the later ones by continuous lines; both are indicated by the same (Arabic) figures. The Roman figures refer to the cells of the second degree; II is the oldest, III the intermediate, IV the youngest, of the latter cells.

6. Diagram of the displacements caused by the next three divisions following the same rule.

7, 8. Stages of development of the scales of *Nephrolepis splendens*.

9—13. The same in *Niphobolus rupestris*.

PLATE XXXIII.

FIGS. 1—6. *Aspidium filix-femina.*

1. A frond which has been torn off, and kept for a long time in a close, warm place, and which has produced an adventitious bud at its base. Natural size.

2. Longitudinal section of a terminal bud, × 250.

3. The apex of the lamina of a half-developed frond seen from above, × 250.

4. Longitudinal section of a young frond, with the rudiment of a root, × 300.

5. The same somewhat more advanced, × 100.

6. Longitudinal section of the apex of a root which has not yet broken through the tissue of the frond, × 250.

7. Longitudinal section of the upper end of the frond of *Struthiopteris germanica*, × 30. On the developed frond, to the left, is seen the rudiment of an adventitious root.

8. The last-mentioned rudiment, × 150.

FIGS. 9—20. *Marattia circutæfolia.*

9. Longitudinal section of the end of a stem, × 10. The small circles distributed through the parenchyma are gum-passages. An adventitious root lies deep down in the cortical tissue. Of the youngest of the two visible fronds there is only a small fragment at the side remaining, to which the corresponding membranous lateral portion of the stipule is attached.

10. Longitudinal section of an adventitious bud of the base of the stipule, × 30.

11, 12. Young fronds of different ages seen from above, × 10.

13, 14. Somewhat older fronds, in longitudinal section, × 10.

15. Lateral segment of the same, showing a stipule in process of development, × 10.

FIG.

16. Transverse section of the place of attachment of a more developed frond. The circle in the middle shows the place of insertion of the cylindrical stipes (within it are the vascular bundles); the rest of the tissue belongs to the stipule.

17, 18. Transverse sections through the stipule and stipes of the same frond, one and two lines higher up.

19. Longitudinal section of a similarly developed frond. Twice the natural size.

19b. Lateral half of the stipule of the latter frond, after the removal of the leafy portion.

20. Apical region of a half-developed frond, seen from above, × 100.

PLATE XXXIV.

1. Swollen end of a runner of *Nephrolepis undulata*, in longitudinal section, × 20.
2. Perfect and growing tuber of the same plant. Natural size.
3. Shoot of a similar tuber, detached from the latter. It has already produced two runners.
4. Longitudinal section of the terminal bud of *Polypodium vulgare*, × 250.
5, 6. Apical aspect of the tips of the stem of the same fern, × 250.
7. Apical view of the tip of the stem of *Polypodium dryopteris*.

FIGS. 8—12. *Platycerium alcicorne.*

8. Transverse section of the perfect stem. Natural size.
9. Transverse section of the stem close under the growing terminal bud. Natural size.
10. Net of vascular bundles of the stem seen from above. Natural size.
11. The same seen from below.
12. Longitudinal section of the bark of a root, × 100.

12b. Some cells of the latter, × 450.

PLATE XXXV.

1. Terminal bud of a very vigorous autumn shoot of *Equisetum limosum*, × 400.
2. Longitudinal section of the end of the bud of a lateral shoot of *Equisetum arvense*, at the beginning of May, × 200.
3. *Equisetum limosum.*—Apical view of an end of a stem divided by a transverse section, underneath the third cell from the apex. The edges of contact of the cells within the stem, underneath the cell of the first degree, are shown by dotted lines. × 500.
4. Similar terminal bud; the section has passed somewhat lower down; × 200.
5. Transverse section of the stem of *Equisetum limosum* close under the apex, × 300.

FIG.

6. Lateral view of a terminal bud of the same species laid bare by two parallel longitudinal sections, × 30.
7. Terminal bud of the same Equisetum exposed by thin parallel sections perpendicular to the axis of the stem. The youngest and the second youngest leaf are uninjured; the rest are cut transversely. × 20.
8. Portion of a very young leaf of *Equisetum limosum* exposed by transverse section through the end of the stem, seen from above, × 300.
9. Lateral view of two tips of a somewhat older leaf; the one to the right is about to fork. × 300.
10. Mother-cell of one of the whorled adventitious shoots of *Equisetum limosum* exposed by two parallel longitudinal sections through the young stem-end. × 300.
11. Longitudinal section of a similar shoot in a somewhat later stage of development, × 300.
12. Longitudinal section of a portion of an older internode, with a fragment of the leaves belonging to it. The section has laid open the cavity of the base of the leaf, in which an adventitious bud is concealed. × 60.
13. Part of a longitudinal section of a young internode of *Equisetum pratense*. In the cells of one longitudinal row annular vessels are formed. The transverse septa of these cells are still present. × 300.

PLATE XXXVI.

1. Left side of a delicate longitudinal section of the apex of a growing delicate shoot of *Equisetum variegatum*, × 300.
2. A portion of the seventh internode (reckoning downwards from the apex), from the same longitudinal section.
3. Longitudinal section of the rudiment of the fruit of *Equisetum limosum* at the beginning of April, × 30.
4, 5. Longitudinal section of the youngest sporangium-receptacle from the same specimen, × 200.
6. Half-developed fruit (at the end of October) of *Equisetum arvense*, in longitudinal section, × 50.
7, 8, 9. Stages of development of the sporangia of the same species, all in longitudinal section, × 300.
10. Transverse section of a young sporangium of the same species, × 300.
11. Group of young primary mother-cells of the spores of *Equisetum variegatum*; two of them are about to divide, × 300.
12. Four spore-mother-cells of *Eq. limosum* adherent to one another, more developed, × 300.
13. Half of a young receptacle, with sporangium of the same species, × 150.

PLATE XXXVII.

FIGS. 1—18, 21, 24. *Equisetum limosum*.

1. Free spore-mother-cell, × 400.
2. Spore-mother-cell, whose primary central nucleus has dissolved, × 300.

FIG.

3, 4, 5. Spore-mother-cells, with two secondary nuclei, between which a flattened agglomeration of granules is gradually being formed. Fig. 3 is × 300, figs. 4 and 5 are × 400.

6. Mother-cells, with four tertiary nuclei, arranged in the angles of a tetrahedron, × 450.

7, 8. Mother-cells divided into four special-mother-cells, × 300.

9. Special-mother-cell divided from its sister-cells, and which has become globular. A spore is just forming in it. × 300.

10 Special-mother-cell, with the globular spore. Upon the inner wall of the special mother-cell the first traces of the two wide spiral threads are visible. × 400.

11. Ripe spore, after the stripping off of the remains of the special-mother-cell (the elaters), crushed in sulphuric acid, × 400.

12. Commencement of germination; numerous chlorophyll-granules are visible in the fluid contents. The central nucleus of the spore has disappeared; in the cell two accumulations of granules are seen, each of which surrounds a secondary nucleus. × 400.

13—18, 21. Differently developed germ-plants, from the beginning to the middle of June, × 300.

24. Fragment of the margin of an older prothallium (in the middle of July), with a half-developed and a ripe antheridium, both shown in longitudinal section, × 200.

FIGS. 19, 20, 22, 23, 25—37. *Equisetum arvense.*

19, 20, 22. Germinating spores developed in water, × 300.

23. Somewhat older prothallium, showing the earliest antheridia, × 150.

25. Portion of the contents of a half-ripe antheridium; small tessellated cells enclose the ellipsoidal mother-cells of the spermatozoa, × 400.

26. A free mother-cell of spermatozoa, × 300.

27. A mother-cell, showing the spermatozoon, × 300.

28. Spermatozoon crippled by treatment with very diluted, watery solution of iodine. The stiffened cilia are already visible, whilst the tail still escapes observation by its undulations. × 500.

29. Spermatozoon quite killed by the same reagent. Its hinder end, already somewhat swollen, is in such a position as to enclose a globe of highly refractive matter; this is of rare occurrence. The membrane of the mother-cell is attached to the frontal turns of the thread. × 500.

30—33. Spermatozoa killed by tincture of iodine. They are far more contracted than those whose motions have ended spontaneously or have been terminated gradually by treatment with a very watery solution of iodine. Great differences are apparent in their size, as appears by the comparison of spermatozoa, drawn with the same magnifying power. × 500.

35. Longitudinal section of a rudiment of an archegonium, × 300.

36, 37. Similar sections of more developed archegonia; fig. 36 × 200, fig. 37 × 300.

PLATE XXXVIII.

EQUISETUM ARVENSE.

FIG.

1. Longitudinal section of an archegonium shortly before the opening of the apex, × 300.
2. The same immediately after the opening, × 300.
3. Perspective view of an archegonium lately opened, shown by means of two parallel longitudinal sections of the prothallium, × 300.
4. Longitudinal section of an archegonium just impregnated, × 300.
5, 7—10. Detached embryos in different stages of development, seen in longitudinal section, × 200.
6. Longitudinal section of an impregnated archegonium, with the embryo in the central cell, × 300.
11. Accidental transverse section of a rudimentary embryo, × 200.

PLATE XXXIX.

1, 2. Longitudinal sections of impregnated archegonia, with embryos; fig, 1, before the falling off of the cells of the mouth; fig. 2, after the same. × 200.

3. Longitudinal section of a lobe of a prothallium, with two impregnated archegonia, × 200.

4, 5. Embryos more advanced, seen in the front, so that both the primary and the secondary axes are in the line of sight, × 200.

6. Longitudinal section of the lower part of a germ-plant, at about the stage of development of fig. 3 in the next plate, × 100.

PLATE XL.

1. Lobe of a highly developed prothallium cut through longitudinally. Besides abortive archegonia, the section has exposed an impregnated one with a considerably developed embryo. × 100.
2. Embryo just breaking through the prothallium, shown in longitudinal section.
3. Portion of a prothallium with a germ-plant, whose root and first leafy shoot have recently emerged from the prothallium, × 10.

PLATE XLI.

FIGS. 1—4. *Ophioglossum vulgatum.*

1. Longitudinal section of a stem at the beginning of December. Above, on the left, is a rudimentary pair of fronds (about ½ inch long), destined for development in the following spring. The section is exactly through the median line of the protuberance of cellular tissue, which is situated somewhat laterally in front of the latter frond, and which encloses the younger fronds. × 20.

FIG.

2. Longitudinal section through the middle line of the frond destined for development in the following spring in the bud-region of a similar stem, × 20.

2ᵇ. The terminal bud and the two youngest fronds of the latter specimen, × 200.

3. Transverse section close above the terminal bud of a similar stem, × 20.

3ᵇ. Transverse section through the same stem, ⅛ line lower down.

4. Transverse section close above the terminal bud, which is seen through the opening of the narrow canal leading to it, × 300.

FIGS. 5—11. *Botrychium Lunaria.*

5. Longitudinal section of a prothallium, × 50. Above, to the right, is an archegonium; on the left of this are five antheridia, of which three are empty.

6. Longitudinal section of antheridia shortly before opening, × 300.

7. Hinder end of a prothallium, with remains of the spore-membrane, × 300.

8—10. Germ-plants with adherent prothallia, × 6. Figs. 8 and 9 seen from the side, fig. 10 from above; *p*, prothallium; *a*, the end of the primary axis of the germ-plant.

10ᵇ. The germ-plant. Fig. 10, longitudinal section, with adherent prothallia; *g*, the end of the bud of the principal axis of the germ-plant. × 30.

PLATE XLII.

1. Germ-plant with prothallium seen from above, × 6.

1ᵇ. The same cut through longitudinally in the direction from *a* to *p*.

2, 3. Abortive germ-plants whose prothallia are already dead, × 6.

4, 5, 6. Normally developed germ-plants, about one year old. Natural size.

7, 8. Germ-plants whose second frond already projects out of the lower first frond, × 2.

9. The same cut through longitudinally, × 20. The first frond has already died down to a hardly perceptible membranous border. In the stipule-like second frond the rudiments of the third and fourth lie concealed.

10. A plant dug up in September, 1854, cut through parallel to the surface of the frond destined for development in the following spring. Natural size.

10ᵇ. The lower part of this specimen, × 20.

10ᶜ. Terminal bud of this specimen, in a position turned from the right to the left, × 300.

11. Section of the bud of a plant in full growth at the beginning of June. The rudiment of the fertile frond is already visible close by the enclosed frond destined for development in the next year but one.

PLATE XLIII.

PILULARIA GLOBULIFERA.

FIG.

1. Longitudinal section of a ripe large spore.
2. Longitudinal section of the upper part of a large spore at the first commencement of germination, × 300.
3. Lateral view of a very young prothallium, × 400.

3^b. The same cut through longitudinally, × 400.

4. Longitudinal section of a germinating spore, with the prothallium still concealed between the lobes of the outer spore-membrane, × 50.
5. Longitudinal section of a young prothallium, × 300.
6. A small spore whose inner membrane has burst and from the fissures in which the mother-cells of spermatozoa are emerging; from some of the latter the spermatozoa are escaping, × 600.

6^b, 6^c, 6^d. Spermatozoa in different positions; 6^b, one which has just made its way out of the mother-cell, × 500.

7. The upper part of a germinating inner spore seen from the outside, with some spermatozoa, × 150.
8. Longitudinal section of a prothallium ready for impregnation, × 500.
9. Prothallium ready for impregnation (or just impregnated?) in longitudinal section. The contents of some of the cells of the covering layer, and also the layer of a portion of the outer spore-membrane, is shown. × 400.
10, 11. Longitudinal sections of prothallia just impregnated, enclosing rudiments of embryos, × 300.
12. Prothallium with a more developed embryo, in longitudinal section, × 300.
13. Embryo of a similar prothallium, × 300.
14. Prothallium with an embryo which is beginning to develope the first frond, in longitudinal section, × 300.
15. Embryo enclosed by the prothallium in the act of forming the first frond and the first root, × 300.
16. Longitudinal section of an abortive prothallium, × 300.

PLATE XLIV.

FIGS. 1—7. *Pilularia globulifera.*

1. Longitudinal section of a prothallium containing an embryo about to burst forth, × 50.
2. Longitudinal section of a spore and germ-plant whose first frond has broken through the prothallium.

2^b. Bud-end of the latter germ-plant, × 300.

2^c. Root-end of the latter germ-plant, × 300.

3. Longitudinal section of a young macrosporangium, × 300.
4. Central cell of the latter, rather more developed, × 300.

FIG.

5. Two spore-mother-cells, and some of the small mucilaginous cells out of the inner cavity of a sporangium destined to form a large spore, × 300.
6. One of the young, large spores, with a set of four abortive special-mother-cells, from a similar sporangium, × 300.
7. A similar sporangium, cut through longitudinally, at the same stage of development, × 200.

FIGS. 8—14. *Pilularia minuta.*

8. Longitudinal section of a very young fruit, × 100.
9. An almost ripe fruit, cut transversely close above the lowest sporangia, × 10.
10. Mother-cell of large spores divided into four special-mother-cells, × 400.
11—14. Stages of development of large spores; by the side of figs. 11 and 12 abortive mother-cells from the same sporangia are drawn. Fig. 11 is × 300, fig. 2 is × 150, and figs. 13 and 14 are × 250.

FIGS. 15—24. *Marsilea pubescens.*

15. Outlines of a large spore just escaped from the opening fruit, in longitudinal section.
16. Apex of the same (the gelatinous covering in this and the following figures is not shown). The primary spore-membrane and the lenticular cell occupying its apex have been carefully drawn out from the introversion of the inner layer of the exosporium. × 300.
17. Commencement of germination. In each lenticular cell two globular nuclei are seen in the place of the primary one. × 300.
18. Bicellular rudiment of a prothallium, laid bare by means of two parallel longitudinal sections through the spore. The primordial utricles of the cells are contracted by the action of a concentrated solution of caustic potash. × 400.
19. Lateral view of a four-celled rudiment of a prothallium, × 400.
20—21. Lateral view of a more developed prothallium, × 300.
22. Prothallium ready for impregnation, in longitudinal section, × 300.
23. Half-developed prothallium, seen from above, × 300.
24. The same from below, × 300.

FIGS. 25—32. *Salvinia natans.*

25. Microsporangium cut transversely; the antheridia (microspores which have shed their outer membranes) are falling out, × 200.
26. A single microspore less developed, × 200.
27—28. Cellular bodies (antheridia) squeezed out of the sporangia with small spores in the middle of March, × 300.
29, 30. Riper antheridia already half emptied, × 300.
31. Spermatozoon with attached mother-cell, × 500.
32. Spermatozoon killed by iodine, × 500.

PLATE XLV.

SALVINIA NATANS.

FIG.

1. Longitudinal section of a large spore at the commencement of germination, × 30.
2. A fragment of the exosporium of a microspore, in longitudinal section, × 300. Three layers are distinguishable. A thin inner layer, a thicker middle layer, and a very thick, apparently cellular, outer layer.
3. A very young prothallium, detached, with a fragment of the inner spore-membrane adhering to it, × 200.
4. The same, the longitudinal section passing through the entire spore, × 200.
5. A more advanced prothallium, in which the first archegonium is developed; in longitudinal section, × 200.
6—7. Longitudinal section of unimpregnated archegonia, in which germinal vesicles are visible, × 300.
8. Transverse section of an unimpregnated archegonium with two terminal vesicles. The observer is looking into it from below, and in the middle of the figure the interior of the mouth of the canal is seen.
9. Fragment of a prothallium cut through longitudinally, in which archegonia are visible, one unimpregnated and the other just impregnated, × 300.
10. Longitudinal section of the angle of a prothallium, exhibiting an archegonium with an unusually long canal, × 300.
11. Three-celled embryo, entirely filling the central cell of its archegonium. The position of the mouth of the canal is shown by two lines. × 200.
12. An impregnated archegonium, with an abnormally large central cell, a small part of the latter only being filled by the few-celled embryo, × 200.
13. An impregnated archegonium enclosing an eight-celled embryo, × 300.
14. A 16-celled embryo detached, *a* from the outside, laterally, *b* in longitudinal section, *c* seen from behind.
15. A somewhat more developed embryo detached, *a* from above, *b* from the side, *c* also from the side turned round 90°. × 20.
16, 17, 18. More advanced embryos; figs. 16 and 18 entirely, and fig. 17 half detached. Figs. 16 and 18 are × 200, and fig. 17 is × 300.
19. Embryo enclosed by the prothallium, × 300.
20. Detached embryo seen from the front surface, × 200.
21. Embryo enclosed by the prothallium. The first leaf is beginning to develope itself above. × 300.
22. Spores with prothallium and embryo somewhat more advanced, in longitudinal section, × 50.
23. A similar embryo, × 200.
24. A similar embryo detached and seen from the front surface of the first leaf, at the lower margin of which the end of the principal axis is clearly visible, × 200.
25. An embryo more advanced, seen half in front. Near the first leaf *a* the principal axis *b*—which is already once forked and is in the act of forking again—is visible; behind it is the hinder end of the germ-plant *c*.

FIG.

25[b]. Front view.
25[c]. View from above. } The same letters represent the same parts.

26. A germinating spore, whose prothallium is broken through by the first leaf (not by the elongating axis of the embryo), × 50.

27. Spore with prothallium and embryo after the elongation of the axis of the latter, × 80.

27[b]. The terminal bud of the latter embryo, × 300.

28. A more developed germ-plant, with spore attached, in longitudinal section, × 150.

29. Terminal bud of a similarly developed germ-plant, seen from above. Near the third leaf, which is still closely folded (to the left in the figure) is seen the end of the principal axis; underneath it are three of its delicate forks, which are developed into the so-called roots.

PLATE XLVI.

ISOETES LACUSTRIS.*

1. A large spore, a fortnight after sowing, and after soaking for several hours in glycerine, seen from above. The first-formed cells of the prothallium appear spread over the inner wall.
2. Longitudinal section of prothallium four weeks after sowing, × 40.
3. Portion of the apex of a prothallium cut through longitudinally, with two archegonia still in process of development, × 300.
4. Archegonia ready for the separation of the angles of contact of the upper three double pairs of cells, in longitudinal section, × 300.
5, 6. Longitudinal sections of archegonia ready for impregnation, × 300.
7. A ripe microspore seen from above (perpendicular to the transverse diameter) × 500.
8. Lateral view of a microspore four weeks after sowing. The mother-cells of the spermatozoa are formed. × 500.
9. Microspore three weeks after sowing. By rolling the spore under the covering glass the exosporium has burst and is pushed on one side. The mother-cells of the spermatozoa entirely fill the inner cavity of the spore. × 500.
10. A small spore, burst, four weeks after sowing. It has already sent forth several spermatozoa; one of them, still partly enclosed by the mother-cell, is seen within the latter in active motion.

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* Plates XLVI to LIII relate to *Isoetes lacustris*, and the letters *a*, *b*, &c., have the following significations:

a Archegonium. *ac* Central cell. *ao* Mouth of the same. *ax* End of the primary axis of the embryo. *cb* Camium. *ct* Back of the stem. *e* Embryo. *fr* Leaves; fr^1 the first, fr^2 the second, leaf of the germ-plant, and so forth. *fv* Vascular bundle. In some cases the vascular bundles passing to the leaves are merely represented by fr^1 &c., and those passing to the roots by r^1, r^2, &c. (so also in fig. 1*b* of Pl. XLIX). *g* Terminal bud; *gc* the apical cell of the latter. *l* Woody mass; *lsp* the upper, and *lnf* the lower, portion of the latter. *lg* The supplementary shoot of the fore-side of the leaf covering the base of the scale. *r* Root. *rc* The cell of the first degree of the root. *v* Sheath of the base of the root.

FIG.

11. A spermatozoon enclosed by its mother-cell, set free by the crushing of a spore.
12. Spermatozoon still partly sticking in the mother-cell, killed by iodine.
13—15. Free spermatozoa in motion. In fig. 14 the spermatozoon drags along a small vesicle at the thin end.
16, 17. Spermatozoa killed by iodine.
18, 19. Archegonia, just impregnated, cut through longitudinally, with two-celled rudiments of embryos. Seen from the narrow side. × 400.
20. A similar preparation; in the lower cell of the embryo-rudiment division is commencing by the appearance of two nuclei, × 400.
21. The apex of a prothallium cut through longitudinally, with one abortive and one impregnated archegonium, which latter encloses the four-celled rudiment of an embryo, × 300.
22. The last-mentioned embryo detached, and seen from the hinder surface. The line *a b* is parallel to the section through the impregnated archegonium.
23. An impregnated archegonium laid open by a longitudinal section parallel to the front surface of the enclosed embryo.
24. Longitudinal section of an embryo; the number of its cells is less than in the preceding figure, but the characteristic extension of the apical cells of the primary axis has already commenced.

PLATE XLVII.

ISOETES LACUSTRIS.

1. A more advanced embryo, cut through longitudinally, × 300.
2. Longitudinal section of a still more advanced embryo, × 200.
3. Longitudinal section of a germ-plant three months old. The apices of the first and second fronds and of the first root are omitted in the figure. × 200.

PLATE XLVIII.

ISOETES LACUSTRIS.

1. Lateral view of a six-months-old germ-plant, × 3.
2. Longitudinal section at right angles to the larger transverse axis of the stem of a four-months-old germ-plant, × 200.
3. Longitudinal section of the stem at right angles to the lateral surfaces of the woody mass of a germ-plant about eight months old, × 200.
4. Transverse section of a one-year-old plant at the height of the terminal bud, × 30.
5. Transverse section of a two-year-old plant at the place of junction of the upper and lower portions of the woody mass, × 10.
6. Transverse section of an abnormal, three-furrowed, about six-years-old, stem of *Isoetes lacustris* at the same place of junction. Natural size.
7. The middle part of the same preparation, × 30.
8. The terminal bud of the same individual seen from above, × 300.

PLATE XLIX.

ISOETES LACUSTRIS.

FIG.

1. Longitudinal section at right angles to the furrow of the stem of a ten-months-old plant, × 30.

1ᵇ. Woody mass and terminal bud of the same, × 300.

2. Transverse section of the middle of the stem of a plant about eight years old. The principal portion of the bark and the two side lobes are omitted. × 20.

3. Rudiment of a scale seen from the surface, × 200.

4. The same more developed.

5. A perfect scale, × 6.

PLATE L.

ISOETES LACUSTRIS.

1. The terminal bud and the upper portion of the woody mass of the stem shewn in Pl. XLIX, fig. 1, × 300.

2. The same parts of a stem cut through at right angles to the indentation, × 250.

PLATE LI.

ISOETES LACUSTRIS.

1. Longitudinal section through the furrows of the stem of a plant eight years old, × 30.

2. Similar section of the lateral surface of the middle region of the woody mass of an older plant, together with a portion of the cambium. One of the cells of the latter—separated from the next wood-cells by three cambial cells—is beginning to become liquefied. × 250.

3. Longitudinal section of a fragment of a vascular bundle from the older part of the bark, × 250.

4. Transverse section near the woody mass of a vascular bundle running to an older frond, × 250.

5. Terminal bud of an eight-years-old plant seen from above, × 200.

PLATE LII.

ISOETES LACUSTRIS.

1. Longitudinal section of the stem (at right angles to its furrow) of a six-years-old plant, × 20.

FIG.

2. Similar section of the apex of a root in which forking has commenced a short time previously, × 400.
3. Half of a forked root in longitudinal section, × 100.
4. Transverse section of a root-tip, × 400.
5. Transverse section of the forking tip of a root, × 400.
6. Fragment of the lower part of the woody mass of an older plant cut through longitudinally in the direction of its larger transverse axis (part of the preparation figured in Pl. XLIX, fig. 1), × 200.
7. Young frond of an older plant seen from the front, × 300.
8. Similar view of a somewhat more developed frond, × 300.

PLATE LIII.

FIGS. 1—19. *Isoetes lacustris.*

1. Longitudinal section of a young fertile frond, × 300.
2, 3. The lower portion of the front surface of a somewhat more developed fertile frond in longitudinal section, × 300.
4. The lower end of a young fruit cut through longitudinally (according to its position it is destined to produce microspores), × 300.
5. Longitudinal section of the base of a frond, which bears a half-ripe microsporangium, × 20.
6, 7. Sets of four adherent spore-mother-cells, × 400.
8—17. Stages of development of the mother-cell of microspores.
8. The mother-cell filled with homogeneous granular protoplasm, in which the central nucleus floats freely, × 400.
9. Accumulations of more firm mucilage—the rudiments of the second nuclei are forming at the two poles of the globular nucleus, × 500.
10. After the absorption of the primary nucleus and the formation of the secondary ones the primordial utricle of the mother-cell becomes contracted, preparatory to its division, × 400.
11. The secondary nuclei are in the act of dissolution, before the division of the cavity of the mother-cell, × 400.
12. A mother-cell divided into two halves by a septum through its equator, × 400.
13, 14. Mother-cells, each with four free tertiary nuclei; those in fig. 13 are in one plane, those in fig. 14 at the angles of a tetrahedron, × 400.
15. Four special-mother-cells united by the mother-cell; produced by the repeated division of the two halves of the mother-cell (the special mother-cells of the first degree). The septa dividing the latter have different inclinations, × 400.
16. A similar preparation. The four special-mother-cells are lying in the same plane, × 400.
17. Set of special-mother-cells arranged decussately in the last stage of formation, immediately before their individualisation. The innermost layer of the much thickened cell-membrane of the special mother-cells is far more highly refractive than the already swollen outer layers. Treatment with tincture of iodine has contracted the primordial utricles of the cells. × 400.

FIG.
18. Young microspores enclosed by the special-mother-cells, × 300.
19. Half-ripe microspores after the absorption of the special-mother-cells, × 300.

FIGS. 20, 21. *Isoetes tenuissima.*

20. Transverse section of the stem of *Isoetes tenuissima* at the height of the lower portion of the woody mass of that species, × 20.
21. Longitudinal section of a stem of the same species, × 20.

FIG. 22. *Isoetes setacea.*

22. Terminal bud of *Isoetes setacea* seen from above, × 300.

FIG. 23. *Isoetes tenuissima.*

23. Longitudinal section of a young root enclosed by the cortical parenchyma, together with a portion of the downward-growing wood and of the cambium adjoining the latter. The contents of the cell of the first degree and of the upwardly directed daughter-cells of the latter are shown. × 300.

PLATE LIV.

FIGS. 1—2. *Selaginella helvetica.*

1. Young fruit in longitudinal section, × 30.
2. Same section of a very young sporangium, × 300.

FIGS. 3—12. *Selaginella hortensis*, Mett.

3. Longitudinal section of the forking end of a shoot, × 30. The last fork to the left is a young fruit-spike.
4. Outline of a longitudinal section of a slightly more developed fruit-spike, × 30.
5. Forking end of a vegetative-shoot, the under side, × 30.
6. End of a vegetative-shoot laid bare by a longitudinal section parallel to the axis; seen from the narrow side, × 50.
7^a. Forked end of a stem, seen from the (wide) upper side, × 80.
7^b. The same, seen from above.
7^c. The same as 7^a, × 350.
7^d. The same as 7^b, × 350.
8. Half of an end of a shoot which has recently forked (like that shown in fig. 5), in longitudinal section, × 500.
9. End of a shoot at the commencement of forking, in longitudinal section, × 350.
10. A similar specimen; the fork is somewhat more advanced.
11, 12. Apices of shoots whose development is almost intermediate between those shewn in figs. 8 and 9; seen from above, × 350.

PLATE LV.

SELAGINELLA HORTENSIS.

FIG.

1, 2. Longitudinal section through that part of the naked end of a young fruit-spike, at which a sporangium is going to be formed, × 500.

3. A very young sporangium in longitudinal section, × 600.

4. A more developed sporangium (destined to form large spores), together with the leaf above it, cut through longitudinally, × 400.

5. Longitudinal section of a more developed sporangium, × 150.

5^b. A portion of the same specimen, × 300.

6. Longitudinal section of a large sporangium, whose mother-cells are beginning to isolate themselves, × 300.

7. Mother-cell of large spores, which has just divided into four special-mother-cells, surrounded by some of its abortive sister-cells, × 400.

8—10. Double pairs of very young large spores, still slightly held together by the last remains of the dissolved special-mother-cells. Fig. 8, × 300; figs. 9 and 10, × 500.

11. A young spherical capsule from the outside; through its walls the four spores, already of a considerable size, are just visible, × 30.

12. A slightly more developed spherical capsule, opened by a longitudinal section, × 50.

12$_b$. One of the spores of the latter, after long soaking in water, × 300.

13. A somewhat more developed large spore, × 300.

14. Transverse section of a more perfect large spore, × 300.

14^b. The same spore treated with a solution of caustic potash. The exosporium is not shown.

15. Half-ripe spore, × 50.

16. Fragment of the wall of a ripe spherical capsule, in longitudinal section, × 200.

16^b. A fragment of the latter wall, seen from the outside. The boundaries of the larger cells of the second inner layer are just visible through the small ones of the upper surface. × 300.

17. Fragment of the membrane (the inner and the outer) of a ripe large spore, cut through longitudinally, × 500.

18. Mother-cells of small spores. The lower one still exhibits the primary central nucleus; in the upper one to the right it is already dissolved; in the upper one to the left are four daughter-nuclei, × 300.

19. A similar mother-cell which has just divided into four special-mother-cells, × 300.

20. A set of four mother-cells arranged tetrahedrically, in each of which a spore is just forming, × 300.

20^b. A similar specimen. The special-mother-cells are placed decussately.

21. First rudiment of a leaf (part of an especially successful longitudinal section of a leaf-bud), × 600.

22, 23. The stages of leaf-development following next after fig. 21, in longitudinal section, × 600.

24, 25. Fore-ends of young leaves seen from the surface, × 300.

FIG.

26. Longitudinal section of the apex of a very young stipule, × 400.
27. Same section of a half-developed stipule, × 200.
28. Outline of a slightly more developed stipule, seen from the surface, × 100.
29. Longitudinal section of the growing apex of a young fruit-branch, × 350.

FIGS. 30, 31. *Selaginella spinulosa.*

30. Rudiment of a fruit in longitudinal section, × 30.
30[b]. Young macrospore.
31. Young macrospore.

PLATE LVI.

FIGS. 1—9, 11 and 12. *Selaginella Galeottii;* 10. *Selaginella Martensi.*

1. End of a shoot bearing only leaves; seen in longitudinal section of the wide side (obtained by adjusting the microscope to the longitudinal axis), × 400.
1[b]. The same, seen from outside.
1[c]. The same, seen from outside the narrow side.
2. Oblique view from above of the end of a shoot, × 400.
3. Longitudinal section of terminal bud parallel to the wide side, × 400.
4. Apex of the same seen from above, × 400.
5. Middle of the fore-edge of a young superior leaf, × 300.
6. Tip of a somewhat more developed inferior leaf, × 600.
7. Fragment of the lateral margin of a perfect inferior leaf, × 300.
8. Fragment of the same, nearer to the mid-rib.
9. A very young stipule seen from the surface, × 500.
10. Adventitious shoot of *S. Martensi*, produced by a fragment of a stem bitten off by wood-lice, × 10.
11. Half of a longitudinal section of a very vigorous shoot of *S. Galeottii*, passing through the median lines of two opposite rows of superior and inferior leaves (the former are to the right in the figure), × 200.
12. Portion of a similar specimen, × 200.

PLATE LVII.

FIGS. 1—12. *Selaginella Martensi.*

1. Mother-cell of large spores, with some of its abortive sister-cells, × 300.
2. A similar mother-cell.
3. Mother-cell of large spores, in which, near the large vanishing primary nucleus, four daughter-nuclei are formed (three only of the latter are visible), × 300.

FIG.

4. Mother-cell, whose primary nucleus is no longer visible; the four newly-formed nuclei lie in one plane, × 300.

4ᵇ. The same specimen treated with watery tincture of iodine. The action of the tincture has separated the four nuclei to some extent from one another.

5. Mother-cell which has already divided into four special-mother-cells, × 300.

6. View from above of a half-ripe spore, × 400.

7. Set of four special-mother-cells, each of which contains a similar half-ripe spore, × 50.

7ᵇ. A similar special-mother-cell, together with its enclosed spore, isolated by gentle pressure with the covering glass, × 400.

8. A young large spore with abnormally developed exosporium, × 400.

9. Mother-cell of small spores, divided into four special-mother-cells, in each of which a spore has originated, × 300.

10. Set of four special-mother-cells, × 400.

11. Set of two vigorous special-mother-cells, and one abortive one, × 400.

12. Cell with abnormally thick walls from a young capsule, × 300.

FIGS. 13—17. *Selaginella helvetica.*

13. Small spore, five months after sowing. In the internal cavity a large number of small globular cells has been formed, × 400.

14. A similar spore subjected to gentle pressure. Some of the above cells have escaped.

15. A similar spore two weeks later, lightly pressed. Each of the escaped cellules now exhibits a very delicate spiral spermatozon.

16. Large spore shortly after sowing; in longitudinal section, × 200.

17. Prothallium seen from above, six weeks after sowing, × 300.

FIGS. 18—23. *Selaginella Martensi.*

18. Inner membrane of a large spore just taken from the capsule, removed out of the exosporium, and viewed perpendicularly to the surface of the rudiment of the prothallium which is attached to its inner side, × 400.

19. Prothallium six months after sowing, in longitudinal section, × 200.

19ᵇ. One of the archegonia of this specimen.

20. Young germ-plant isolated, and cut through longitudinally, × 200.

20ᵇ. The spore, from the interior of which this germ-plant was taken. The distended prothallium enclosing the somewhat developed embryo, projects far out of the fissures of the apex of the spore-membrane, × 15.

21. An unfolded germ-plant, drawn out of the spore, × 3.

21ᵇ. The prothallium in which it originated, taken out from the exosporium, × 3.

22. Germ-plant whose first leaves have been removed (the stipules of the latter are remaining), together with the prothallium freed from the outer spore-membrane, × 30.

23. A germinating spore, in whose prothallium (which projects from the outer spore-membrane) two germ-plants have originated, × 5.

PLATE LVIII.

SELAGINELLA DENTICULATA.

FIG.

1. Longitudinal section of an unimpregnated prothallium, eleven months after sowing. Several archegonia have been exposed by the section; in one of them the spherical cell produced in the central cell is represented, × 250.

1ᵇ. Mouth of an archegonium, seen from above, × 350.

1ᶜ. Aperture of an archegonium, where the cells are extended upwards in a papillate manner; seen obliquely from above, × 150.

2. Archegonium whose upper cells are still in close connection. The free spherical cell is not yet formed in the basal cell, × 600.

3. An archegonium just impregnated, laid open by a very successful longitudinal section. The mother-cell of the embryo is divided by a transverse septum. Unfortunately the specimen was spoilt before the drawing was finished. A portion of the cellular tissue of the prothallium has been drawn from recollection. Ineffectual attempts have been made to obtain another similar specimen, × 600.

4. An impregnated archegonium; in a longitudinal section, which has exposed the archegonium in which the rudiment of the embryo has originated, and also the course of the proembryo which has formed the suspensor. × 200.

5. A similar preparation in which the apex of the second axis of the embryo—which is destined to develope leaves—is turned towards the observer, × 150.

6. A young embryo detached, with a uni-cellular suspensor (a rare case), looking upon the wide side of the second axis, × 500.

7, 8. Similar preparations seen from the narrow side, × 500.

9. From the wide side; 10. from the narrow side of the second axis, × 500.

11. Outlines of a prothallium, in which the embryo lies concealed, which latter has already begun to form its cotyledons, × 30.

12. Longitudinal section of a spore whose embryo has lately broken through the prothallium; its leaves are beginning to turn green. The section has carried away the larger part of one cotyledon, its stipule, and several leaves of the two rudimentary axes of the third degree of the embryo, × 30.

PLATE LIX.

1—5. Mother-cells of the pollen of *Pinus balsamea*, × 300; fig. 1, at the end of March; figs. 2—5, in the first half of April.

6. Pollen-mother-cell of *Pinus Larix*, divided into six special-mother-cells; beginning of March, × 300.

7. Pollen-cell of the same *Pinus* on the 21st March, after treatment with a solution of caustic potash. The second nucleus is already formed.

FIG.

8. A similar pollen-cell, already divided into two cells, treated with caustic potash and freed from the exine by rolling under the covering glass, × 300.
9. Pollen-cell of *Pinus Larix*, taken from the nucleus of an ovule in the middle of May. The exine has been stripped off by the swelling of the intine, × 400.
10. Longitudinal section of an ovule of a cone of *Pinus Austriaca* (just opened) at the beginning of June, × 150.
11. Longitudinal section of the nucleus of an ovule of *Pinus Mughus* from a cone just in flower, × 300.
12. Embryo-sac of the same species, somewhat later, after the dissolution of the central nucleus, × 500.
13. Embryo sac of *Pinus sylvestris* with the neighbouring cells, which are becoming detached; beginning of June, × 500.
14. Longitudinal section of the nucleus of the ovule of a cone of the same species which has lately flowered (beginning of June). The pollen-tube has already penetrated rather deeply into the nucleus, × 100.
15. Fragment of a detached embryo-sac of *Pinus Austriaca*, in the middle of June. Numerous free secondary nuclei are attached to the inner wall, × 300.
16. Longitudinal section of the embryo-sac of *Pinus sylvestris*, filled with cellular tissue; end of June, × 300.
17. Ovule and basal portion of the spermophore of *Pinus maritima*, at the beginning of January of the second year. The walls of the cells of the very advanced endosperm (E) are much thickened by the addition of layers of gelatine. Two pollen-grains (P) have emitted tubes for a short distance only into the nucleus, × 50.
18. A single cell of the endosperm at the same time, treated with tincture of iodine. The primordial utricle of the cell is contracted, × 300.
19. A single cell of the endosperm of the same species in the middle of March. The thickening layers of the cell-wall are already almost dissolved; only the primary membrane of the cell is still intact, × 300.
20. Fragment of the membrane of the embryo-sac of *Pinus Strobus* cut through longitudinally, with some endosperm-cells loosely attached to the inner side; at the beginning of April, × 300.

PLATE LX.

1. Longitudinal section of the embryo-sac of *Pinus sylvestris*, at the beginning of April of the second year, × 30.

1a. One of the cells of the interior, × 300.

2. Embryo-sac detached, at the beginning of May. A layer of newly-formed cells has attached itself firmly to the inner side of the hardened membrane of the embryo-sac, which has now entirely displaced the loosened cells of the surrounding portion of the nucleus, × 30.

2a. Portion of the outer side of the embryo-sac of the latter figure, × 300. It will be seen that the cells attached to the inner wall of the embryo-sac are not yet firmly attached to one another at the surfaces of contact with the latter.

FIG.

3. Portion of the membrane of a similar embryo-sac ruptured by gradually increased pressure. Numerous actively-multiplying cells are forced out from the fissure of the membrane; the cells also attached to the inner side of the wall have been detached from it by the pressure, × 200.

4. Longitudinal section of an embryo-sac, for the second time partly filled with cellular tissue; in the middle of May of the second year. The detached membrane of the embryo-sac lies in folds near it, × 50.

5. Young corpusculum, detached, with some of its neighbouring cells; at the end of May. At this time the connection of the individual cells of the endosperm is still very loose, × 300.

6. Longitudinal section of the upper part of an endosperm; end of May. Two young corpuscula are visible. The cells covering the apex of the latter have not yet divided by cross longitudinal septa, × 150.

7. Transverse section through the same part of the less developed endosperm, on May 27th. The observer is looking from below into four corpuscula opened by the section. The large nuclei attached to the inner arch of the apex are visible, × 200.

8. Longitudinal section of a corpusculum at the beginning of June, × 200.

8^b. The rosette of cells covering the apex of the corpuscula, seen from above, × 200.

9. Longitudinal section of a corpusculum, at the top of which the end of a pollen-tube has just arrived, × 200.

10. The lower end of a corpusculum just impregnated, with the germinal vesicle pressed into the arch (on the 16th June), × 300.

11—13. Stages of development of the pro-embryo (the lower ends of the longitudinally-divided corpuscula), from the 16th to the 18th June of the second year, × 300.

PLATE LXI.

1. Apical arch of a longitudinally-divided corpusculum of *Pinus Abies*, L. (*Pinus excelsa*, DC.), at which the end of a pollen-tube has lately arrived, and in which several germinal vesicles adhere, of which one has increased largely in size; on the 23rd June (1858), × 500.

2. Longitudinal section of the upper part of an endosperm of the same species at the same time. Two impregnated corpuscula are opened by the section. In the one to the right the rudiment of a pro-embryo is pressed into the lower end; in that to the left a similar rudiment is still at some distance from the base, × 40.

2^b. The rudiment of the pro-embryo of this latter corpusculum, × 500.

FIGS. 3—11. *Pinus Strobus.*

3. A germinal vesicle just impregnated; on the 26th of June, × 200.

4—7. A series of stages of development of the pro-embryo, arranged according to their state of advancement (from 25th to 28th June). Figs. 4—6, × 300; fig. 7, × 200.

8. The pro-embryo immediately before dividing into four longitudinal rows of cells, × 100.

FIG.

9, 10. Pro-embryos during the division into their longitudinal rows of cells; on the 30th June, × 100.

11. (The middle figure.)—One of the fourth parts of the pro-embryo, at whose lower end the multiplication in the direction of the thickness has begun, × 100.

FIG. 11 (left-hand figure) to FIG. 14. *Pinus Larix.*

11. (Left-hand figure.)—End of a pollen-tube drawn out from the corpusculum, which has been just impregnated.

11^b. The same object after its apex and the cell hanging to it have been pushed out.

12. Apex of a pollen-tube, and portion of the cell attached to it, × 400.

13, 14. Longitudinal section of corpuscula just impregnated, × 150.

PLATE LXII.

FIGS. 1—8. *Pinus Canadensis.*

1. The upper part of an endosperm shortly before the arrival of the pollen-tube at the embryo-sac (on the 7th July of the first year), with two corpuscula laid open by the section, × 200.

2. Longitudinal section of a corpusculum, into which a pollen-tube has lately penetrated (beginning of July), × 200.

3. Longitudinal section of an endosperm (middle of July). It exhibits two corpscula. A pollen-tube has shortly before penetrated to the upper surface of the left hand one. Against the base of this corpusculum the four-celled rudiment of the embryo is compressed, × 200.

4. A recently impregnated germinal vesicle (middle of July) confined at the lower end of the corpusculum, which has been cut through longitudinally, × 400.

4^b. The same specimen treated with an alkaline ley.

5. Longitudinal section of a corpusculum containing a rudimentary pro-embryo pressed into the base, and another less developed one floating freely, × 100.

7. A further developed pro-embryo. The walls of the upper cell, which are are turned towards the corpusculum, are much thickened by the addition of glassy transparent layers, × 300.

8. A more developed pro-embryo. In its upper cells are found spherical irregular masses, of a glassy substance. The wall of the corpusculum—which is detached from the neighbouring cells, and is adherent to the specimen—exhibits shallow pits, and flat ridges, seated on the outer side, whose course corresponds with that of the edges of contact of the neighbouring cells (end of July), × 300.

FIGS. 9, 10. *Pinus sylvestris.*

9, 10. Young embryos in longitudinal section; from the 28th June until 7th July, × 250.

FIG. Fig. 11. *Pinus balsamea.*

11. Longitudinal section of the embryo-sac of *P. balsamea*, filled by a few large cells; at the beginning of May of the first year.

PLATE LXIII.

Figs. 1—12. *Taxus baccata.*

1. Longitudinal section of an ovule at the end of March. The shaded part shows the position of the cells destined to become embryo-sacs, × 30.
2. The cells of this part, × 300. The contents of the rudiments of the embryo-sacs are contracted by tincture of iodine.
3. Apex of the ovule in the middle of April, in longitudinal section. The course of the pollen-tube, which at this time is very delicate, is exposed, × 150.
4. The embryo-sac and neighbouring cells from an ovule cut longitudinally; end of April, × 300.

5—7. Further developed embryo-sacs; detached (6th May), × 300.

8. Embryo-sac and one of its neighbouring cells; detached (17th May), × 500.
9. Embryo-sac; detached, × 300.
10. Longitudinal section of the nucleus of an ovule, through which two pollen-tubes have penetrated to the embryo-sac (22nd May), × 200.
11. Lower end of a pollen-tube with a portion of the endosperm cut through longitudinally; both detached. Impregnation has not yet occurred; the rosette is still uninjured, × 350.
12. Young rudiment of a pro-embryo with a portion of the membrane of the corpusculum detached, × 350.

Fig. 13. *Taxus Canadensis.*

13. Apex of the endosperm with the end of the pollen-tube and an impregnated corpusculum with the rudiment of a pro-embryo in longitudinal section; on the 10th June, × 300.

PLATE LXIV.

Fig. 1. *Taxus Canadensis.*

1. Longitudinal section of the upper end of an endosperm with the pollen-tube; on June 5th. Two corpuscula are laid open by the section; the right hand one is impregnated; the impregnated germinal vesicle occupies the lower third part of it, × 300.

Fig. 2. *Taxus baccata.*

2. Lower ends of two pollen-tubes with portions of the endosperm, which has been cut through longitudinally, soon after impregnation. The pollen-tubes are drawn away for a short distance from the endosperm; the left hand one has in consequence been torn at the outermost apex, × 300.

FIGS. 3, 3ᵇ, 4. *Thuja orientalis.*

FIG.

3. End of a pollen-tube, detached, × 250.

3ᵇ. Some of the contents of the pollen-tube shown in fig. 3, × 500.

4. End of a pollen-tube detached, × 250.

FIGS. 5, 6. *Juniperus Siberica.*

5. Nucleus of the ovule with the lower portion of the integument of the ovule, in longitudinal section; on June 5th of the first year, × 300.

6. Detached embryo-sac at the end of May of the second year, which has become filled with cellular tissue for the second time. The membrane of the embryo-sac is swollen with water, × 60.

PLATE LXV.

FIG. 1. *Juniperus Sibirica.*

1. Apex of the embryo-sac filled with endosperm, in longitudinal section; three corpuscula are exposed; on June 9th of the second year, × 300.

FIGS. 2—7. *Juniperus communis.*

2. Corpuscula cut longitudinally, with a small portion of the endosperm and the pollen-tube; on the 20th July, × 300.

3. Three impregnated corpuscula, with the lower portion of the pollen-tube (longitudinal section of an endosperm on July 28th), × 300.

4. Pro-embryo consisting of three longitudinal rows of cells.

5. Longitudinal section of an impregnated ovule (the integument is omitted in the drawing). The pointed line in the endosperm shows the boundaries of the region in which the cells are loosened and partly dissolved. The development of the embryos of this specimen corresponds almost with that of the one shown in fig. 7. (Beginning of August.) × 30.

6. Lower end of one of the isolated longitudinal rows of cells of a pro-embryo, with the mother-cell of the embryo still undivided, × 150.

7. A similar specimen, with a more developed rudiment of the embryo.

8. A similar specimen.

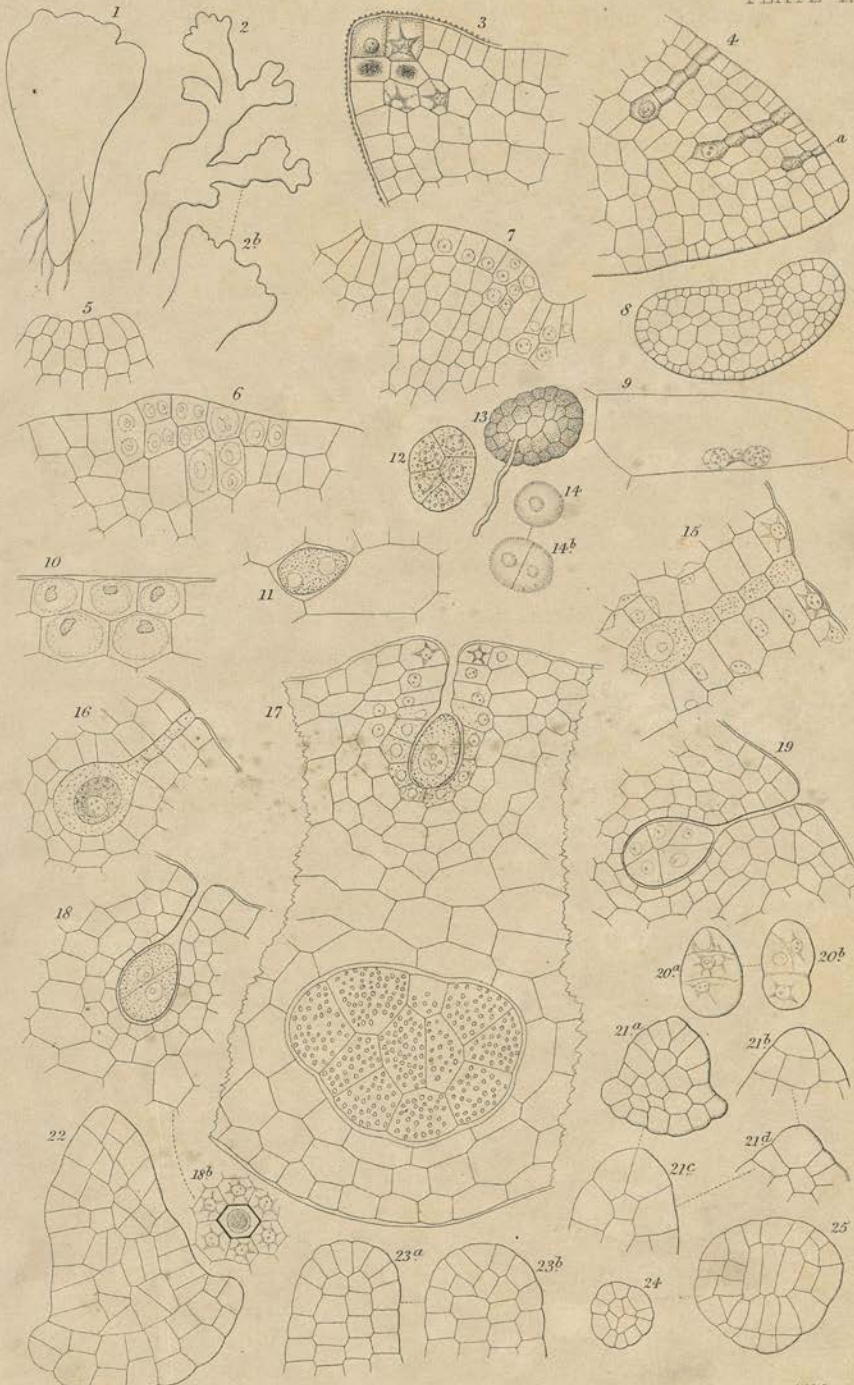
FIGS. 9—10ᵇ. *Thuja orientalis.*

9. Upper end of the endosperm with the group of corpuscula and two pollen-tubes which have penetrated into the depression above it, in longitudinal section; on June 18th, × 250.

10. A similar specimen with a single pollen-tube, which has sent prolongations into the corpuscula; on June 28th, × 250.

10ᵇ. The pollen-tube of the latter preparation detached.

PLATE I.



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W. West imp.

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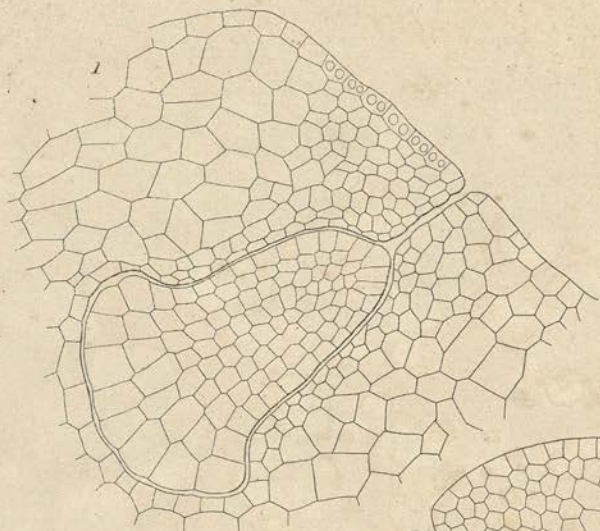

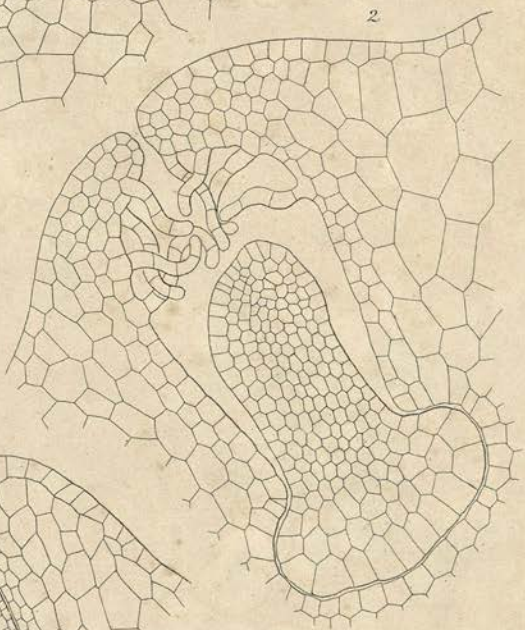

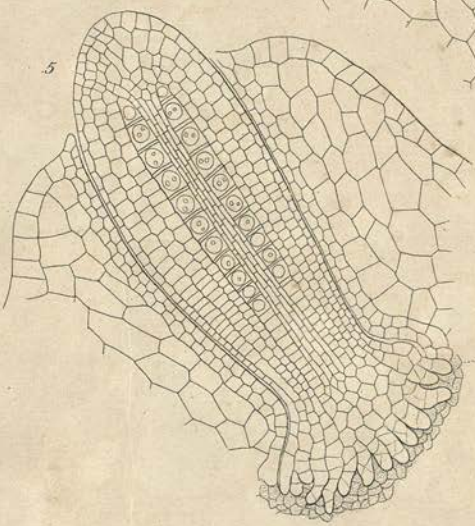

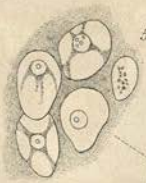

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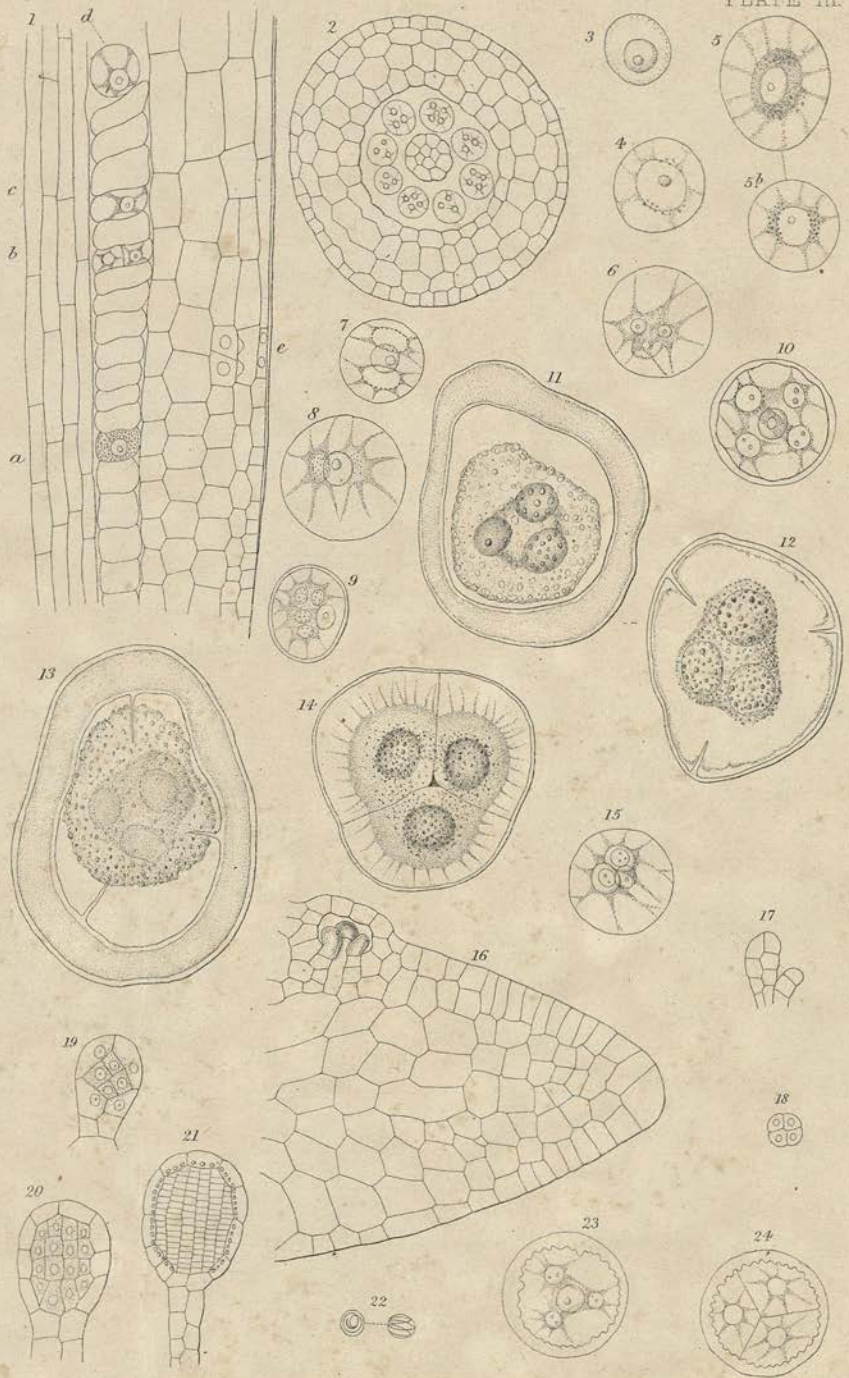

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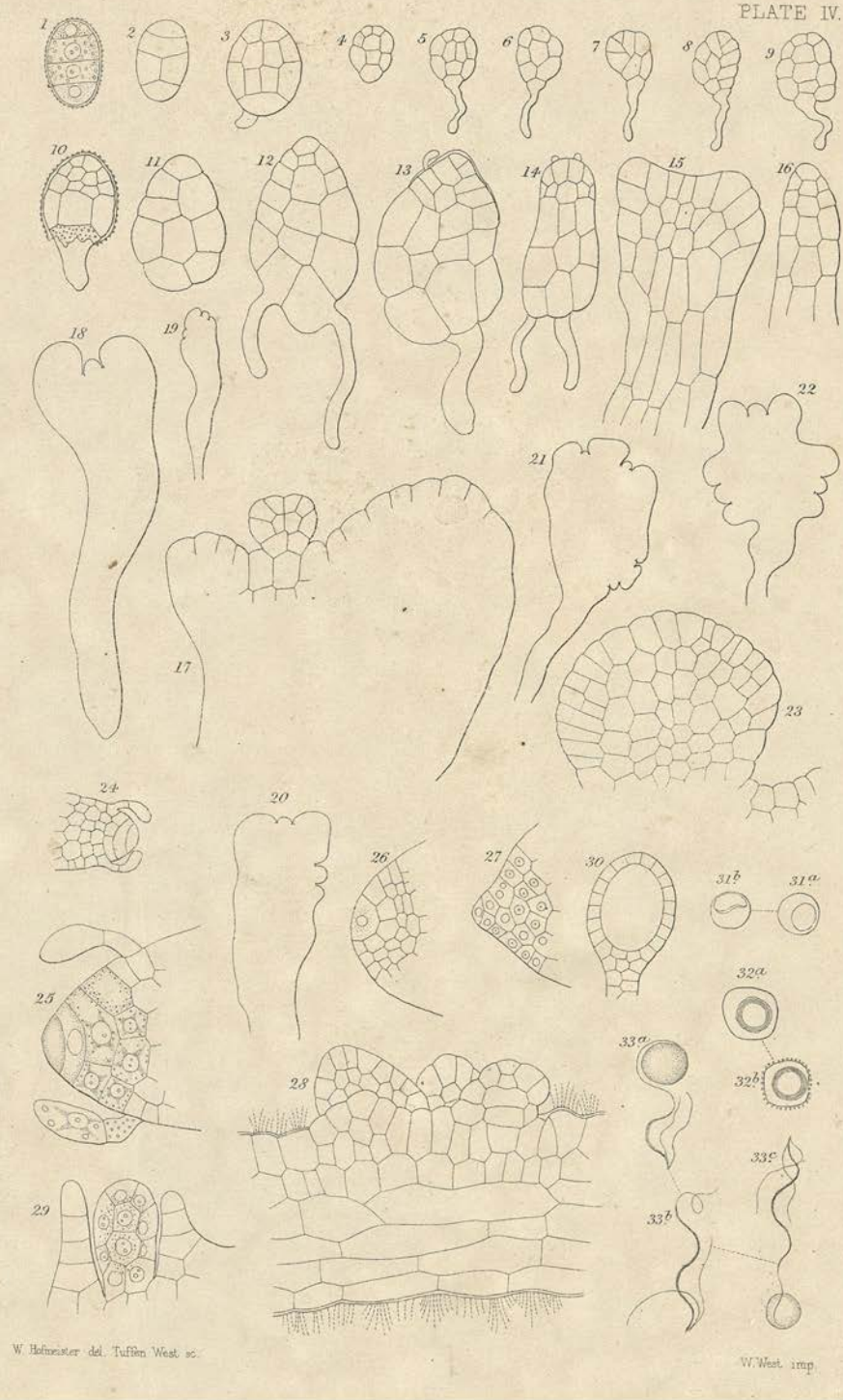

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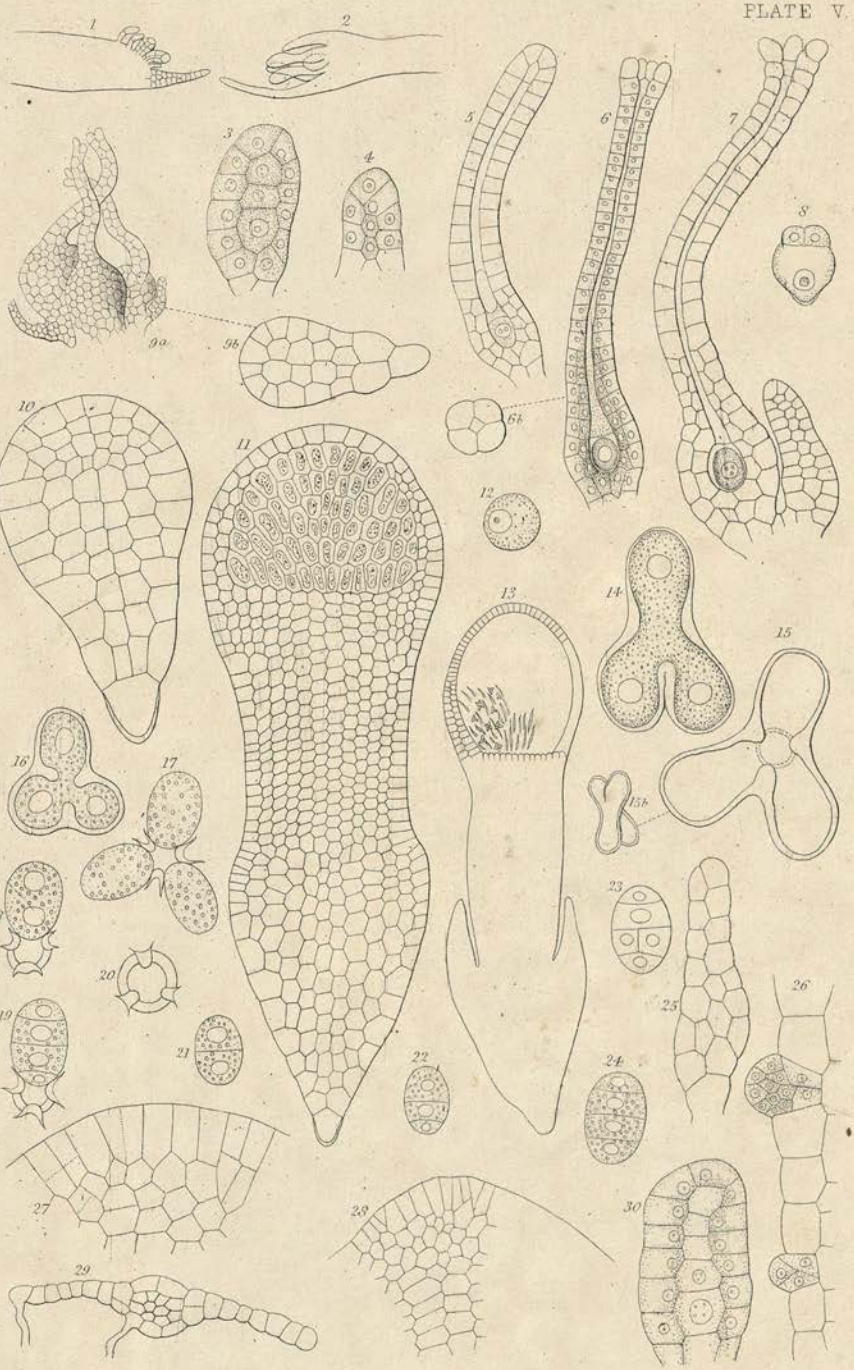

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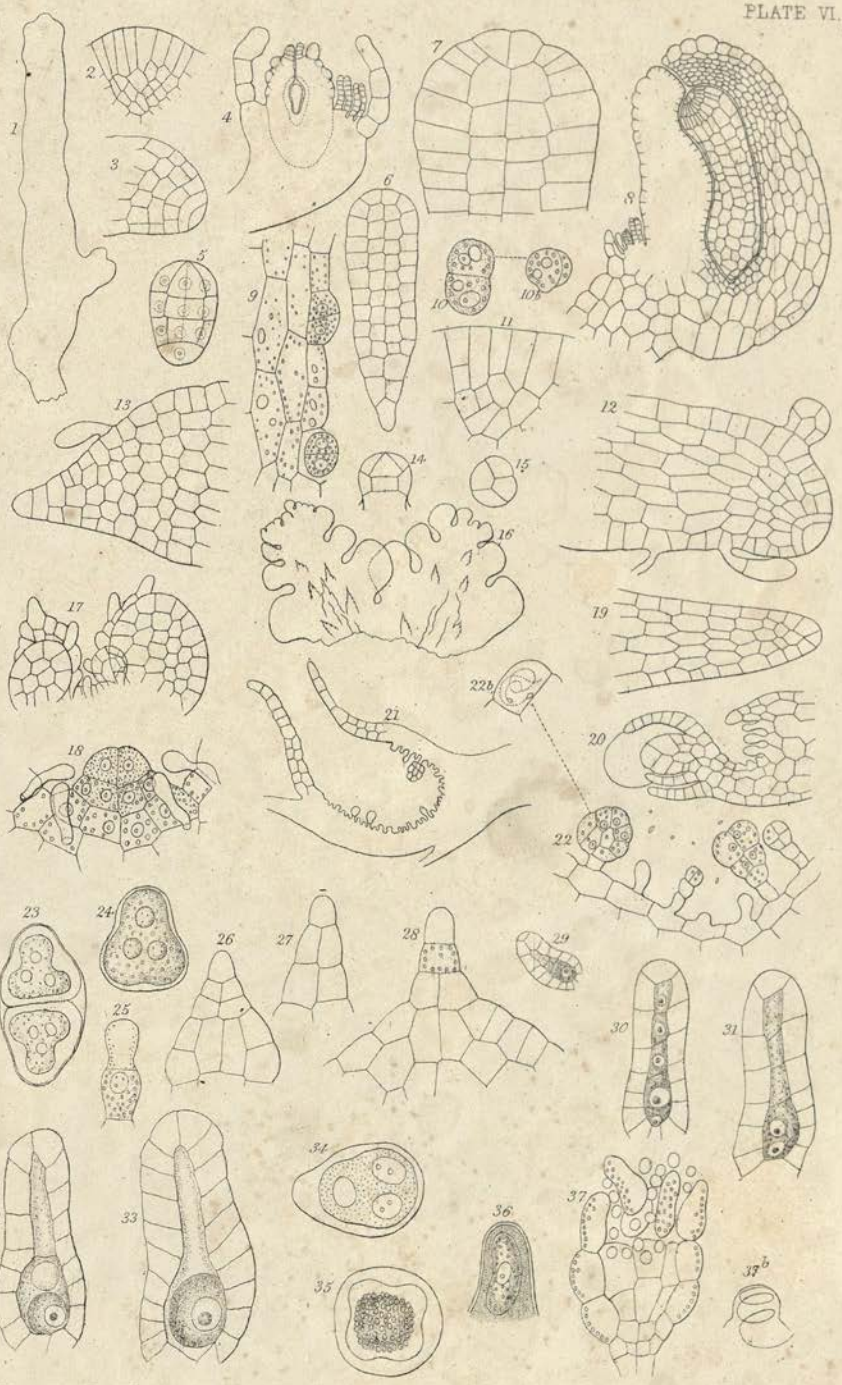

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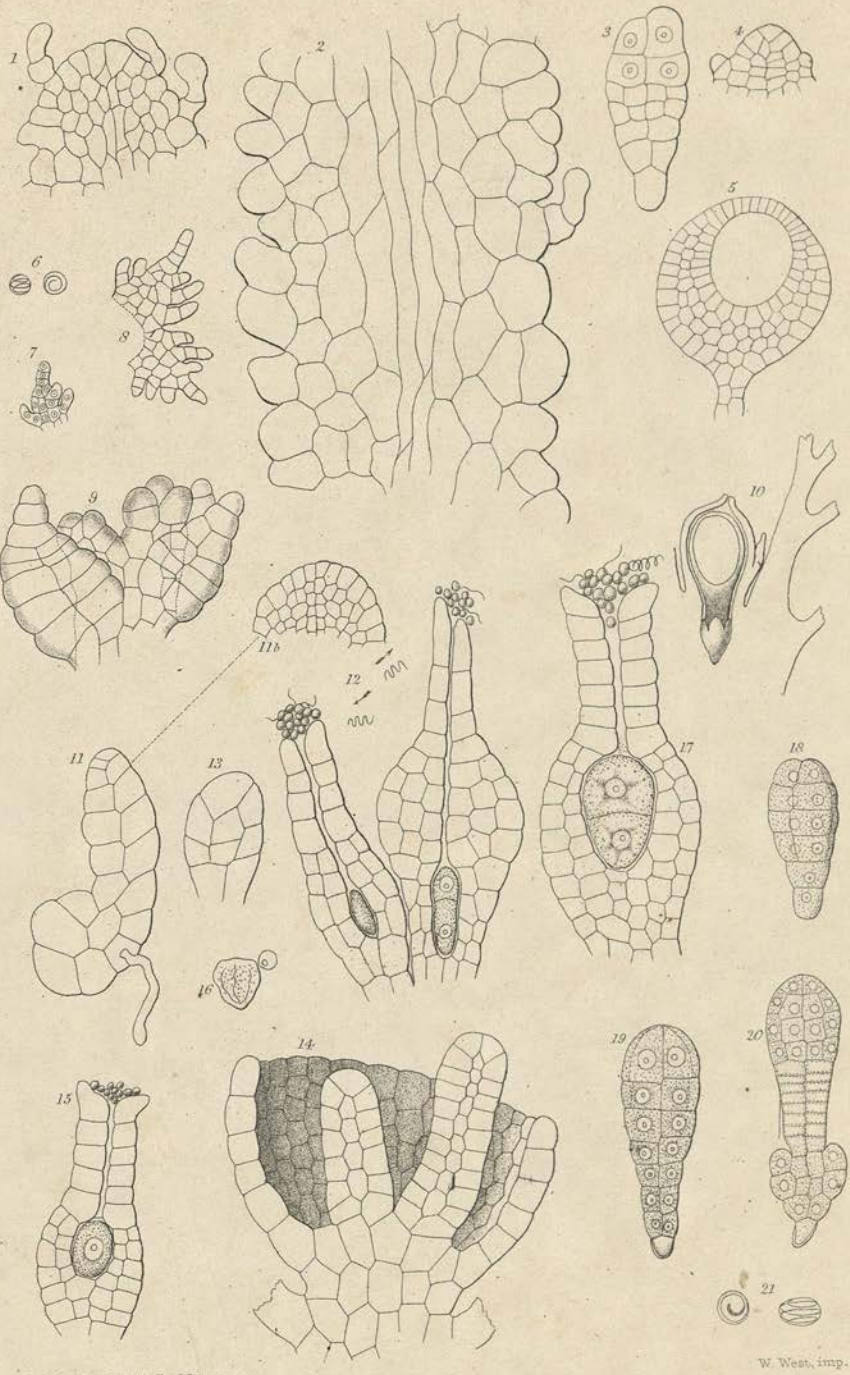

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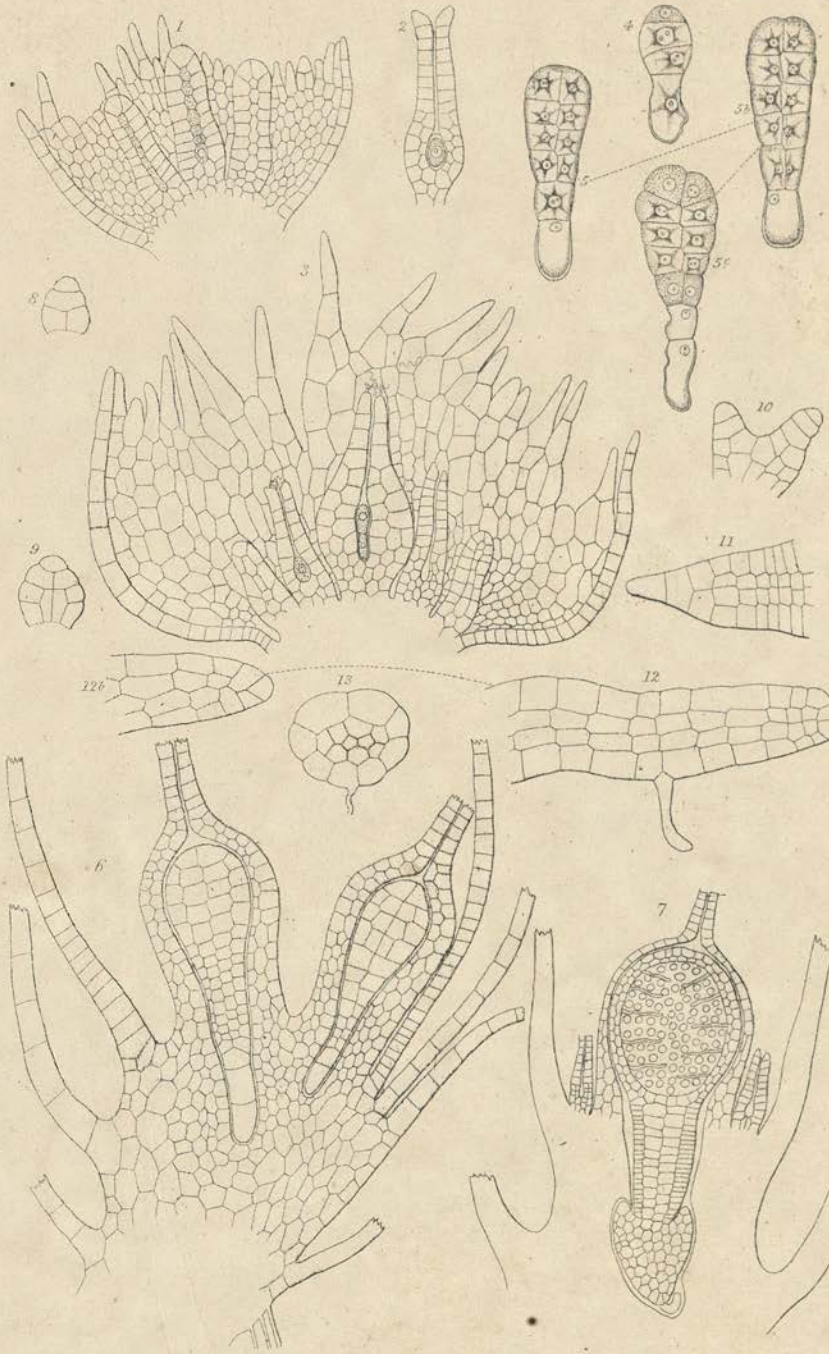

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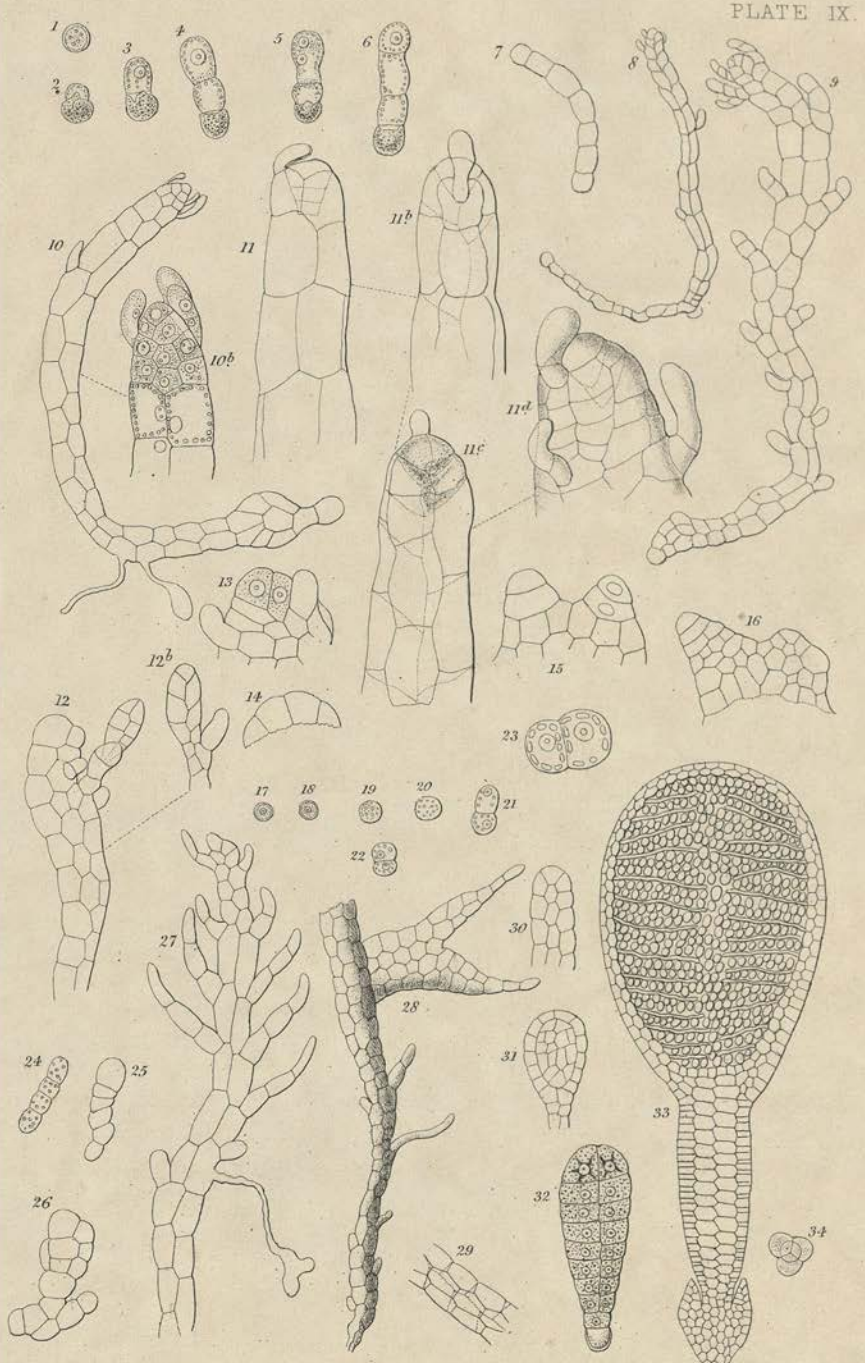

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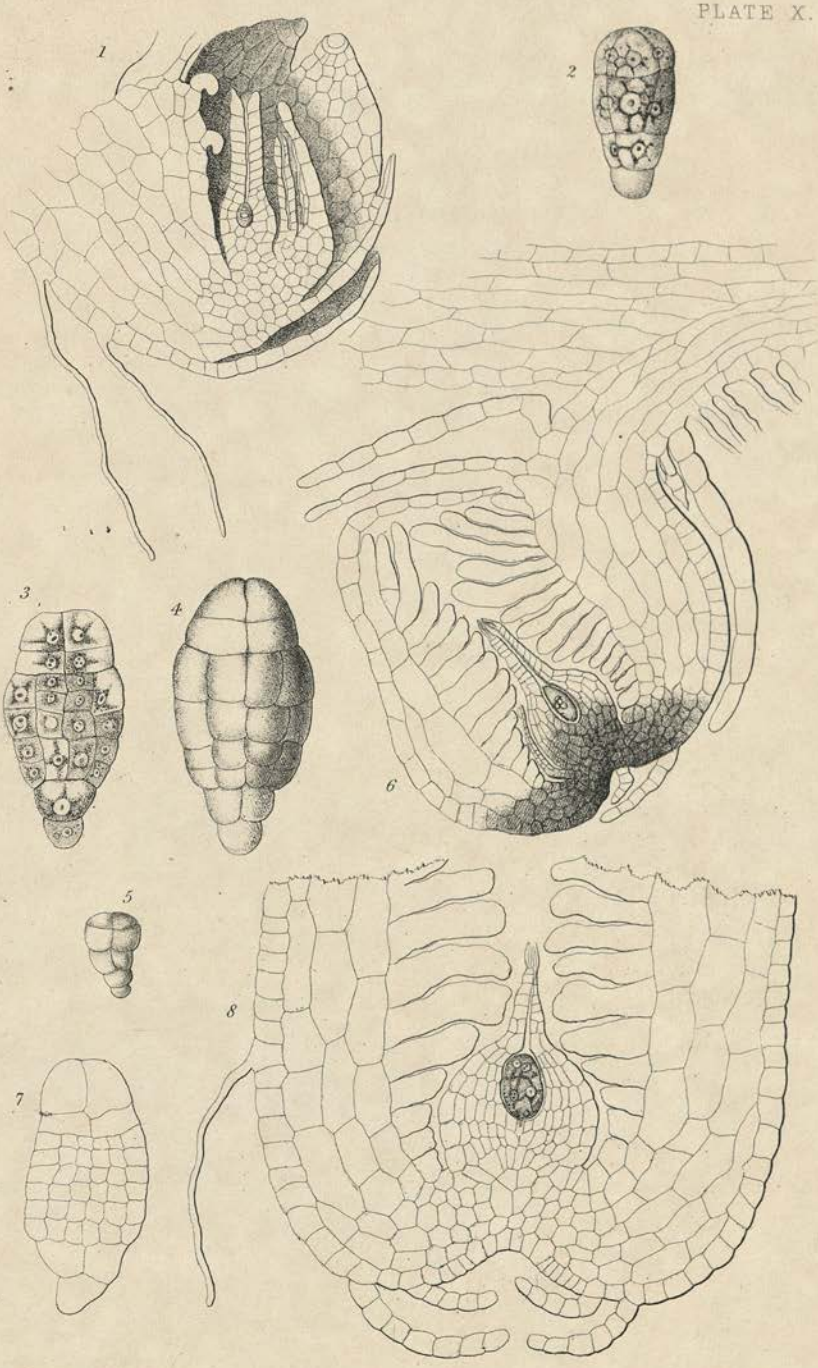

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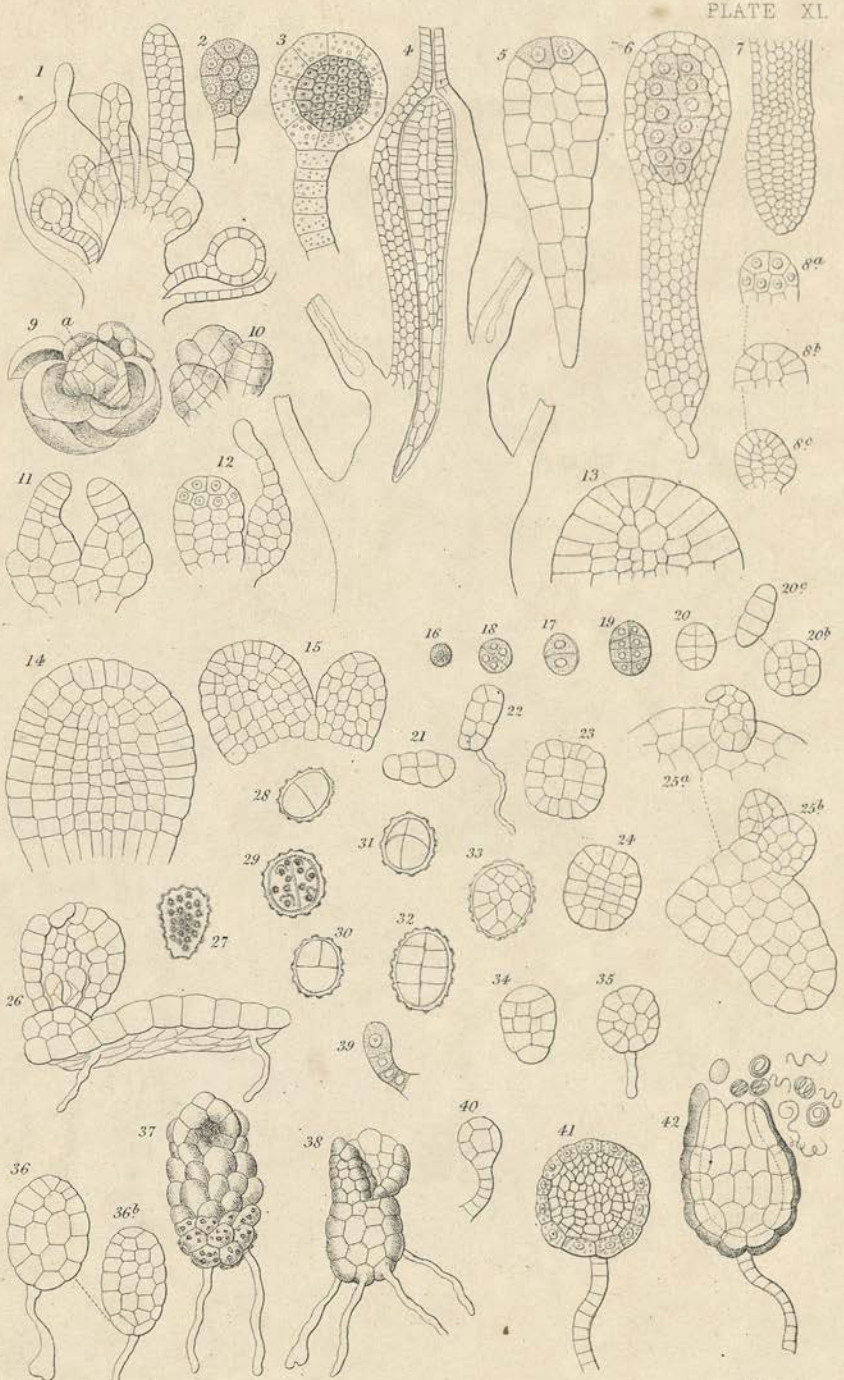

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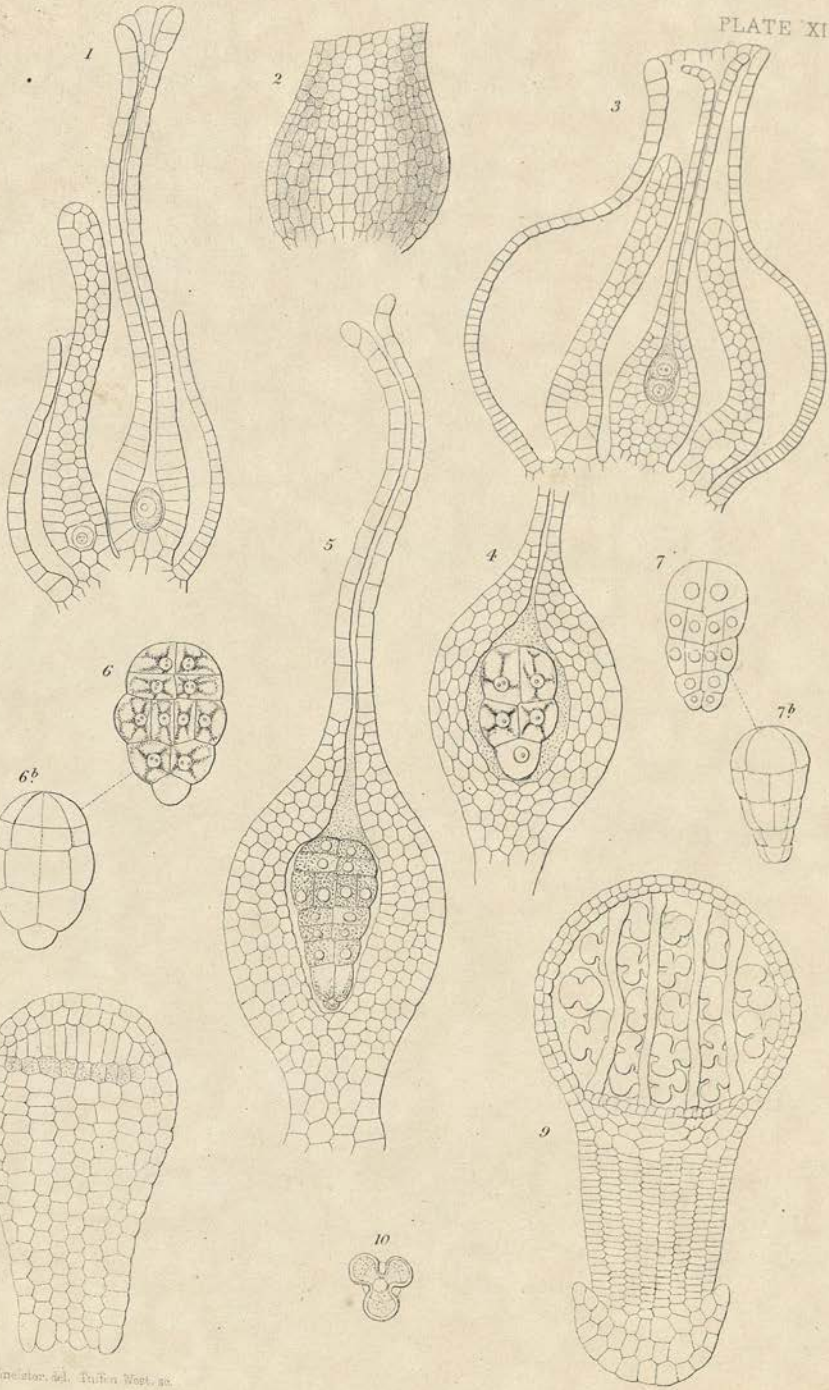

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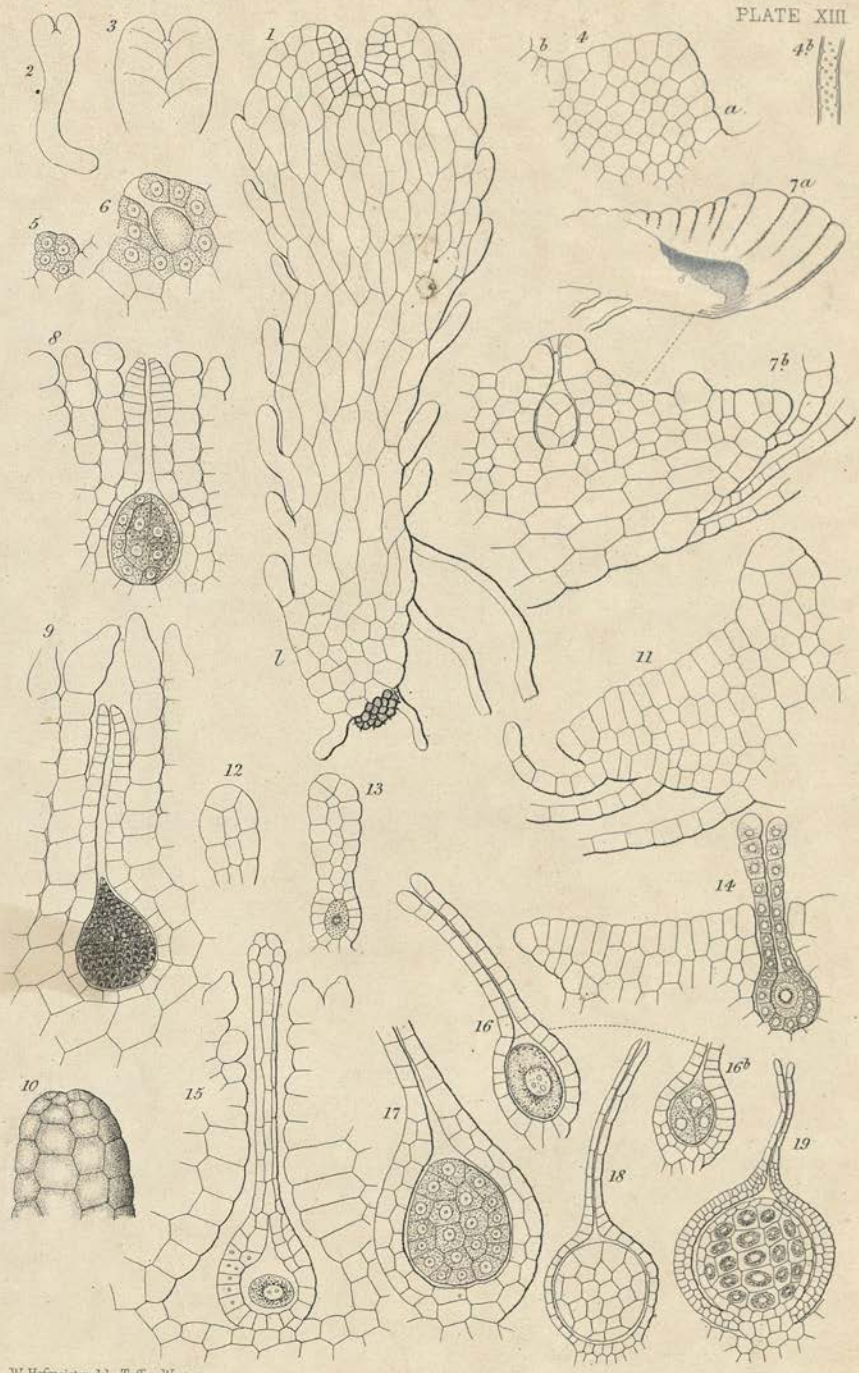

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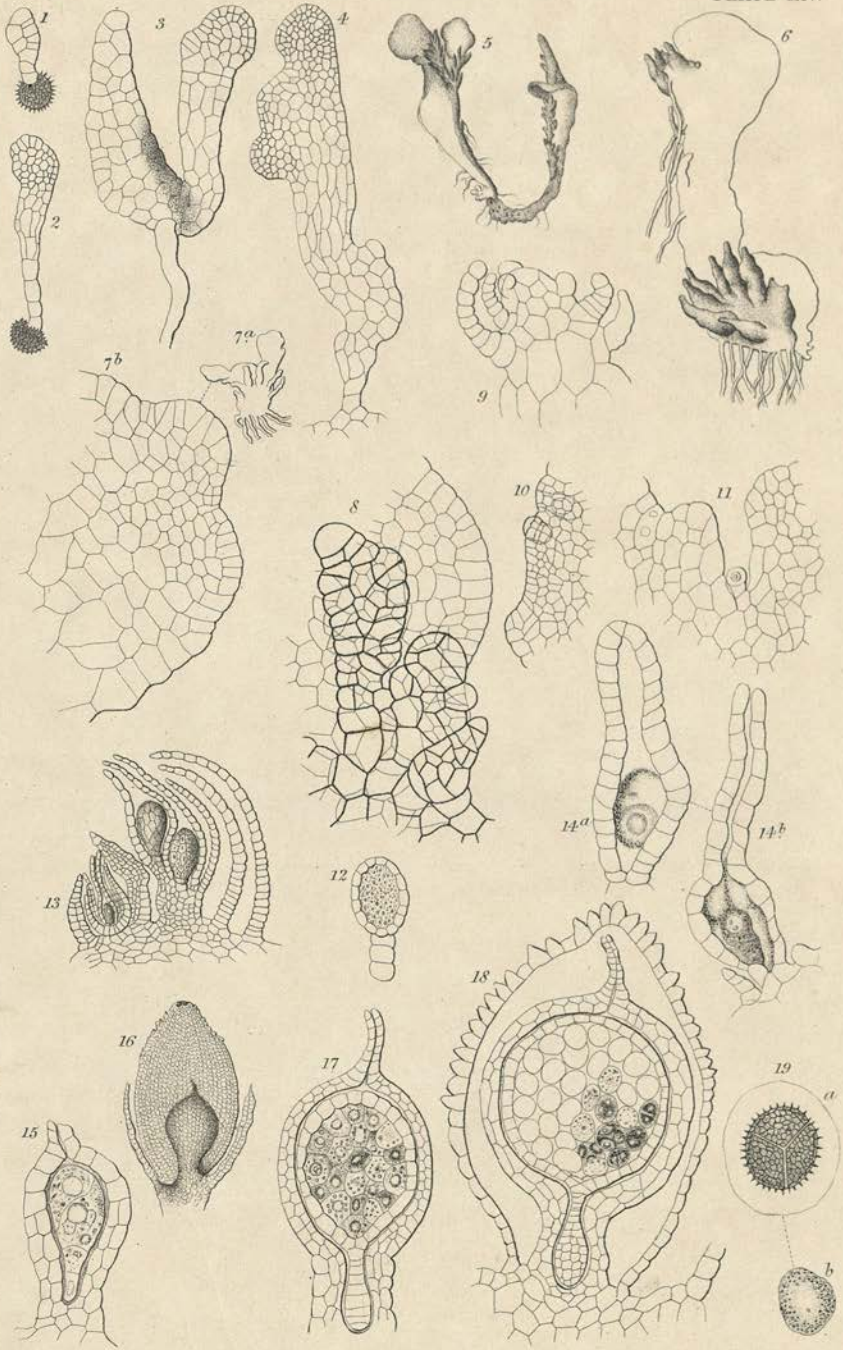

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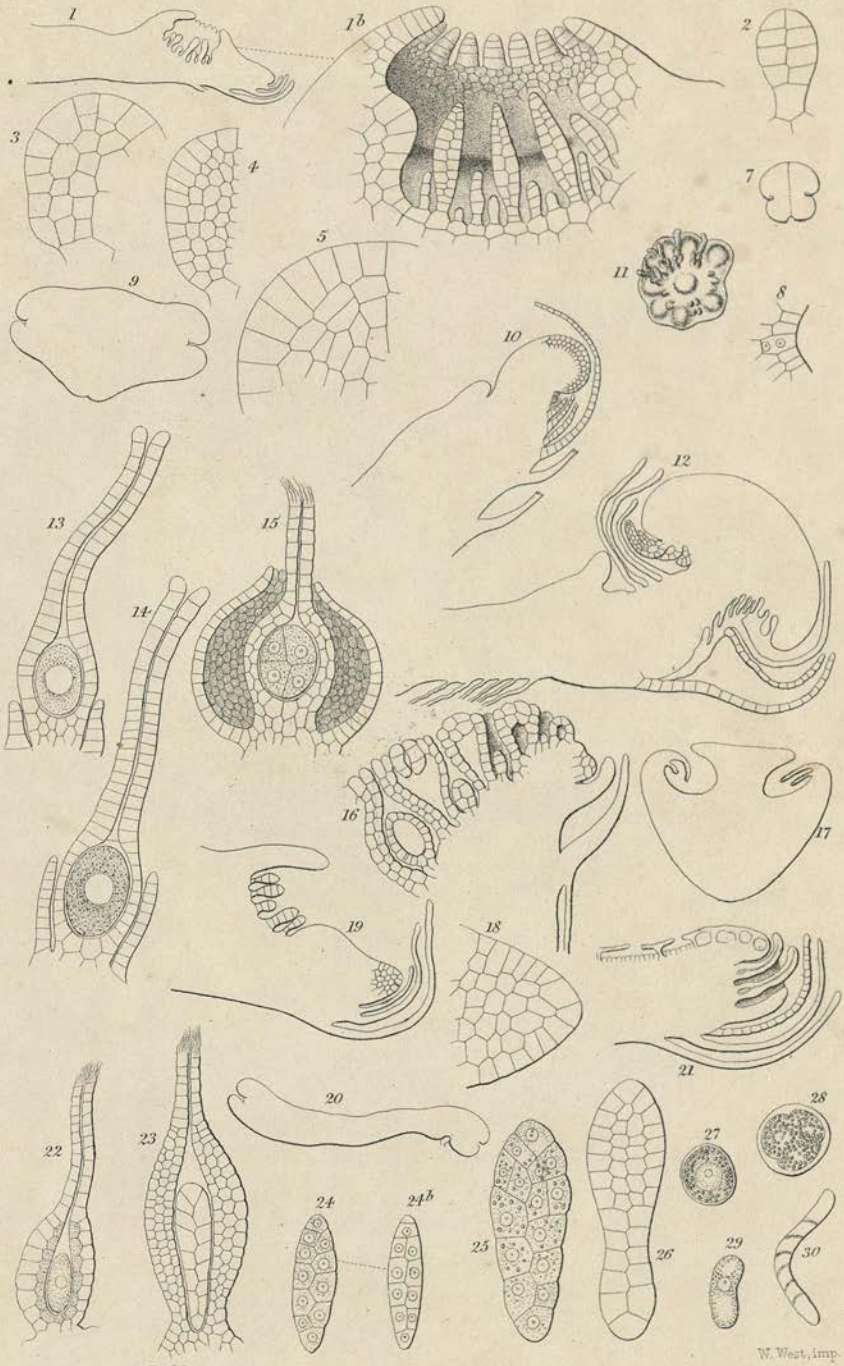

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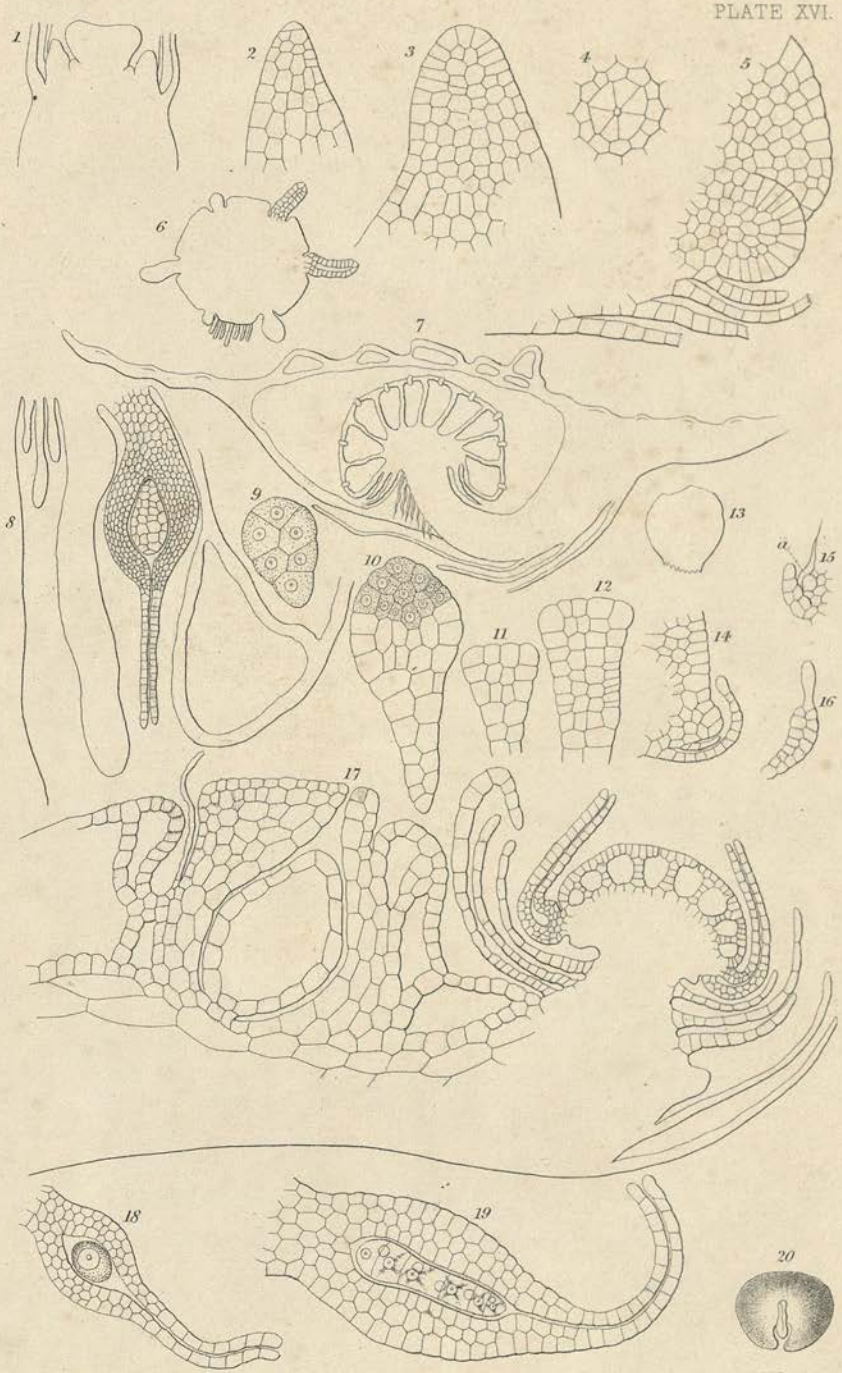

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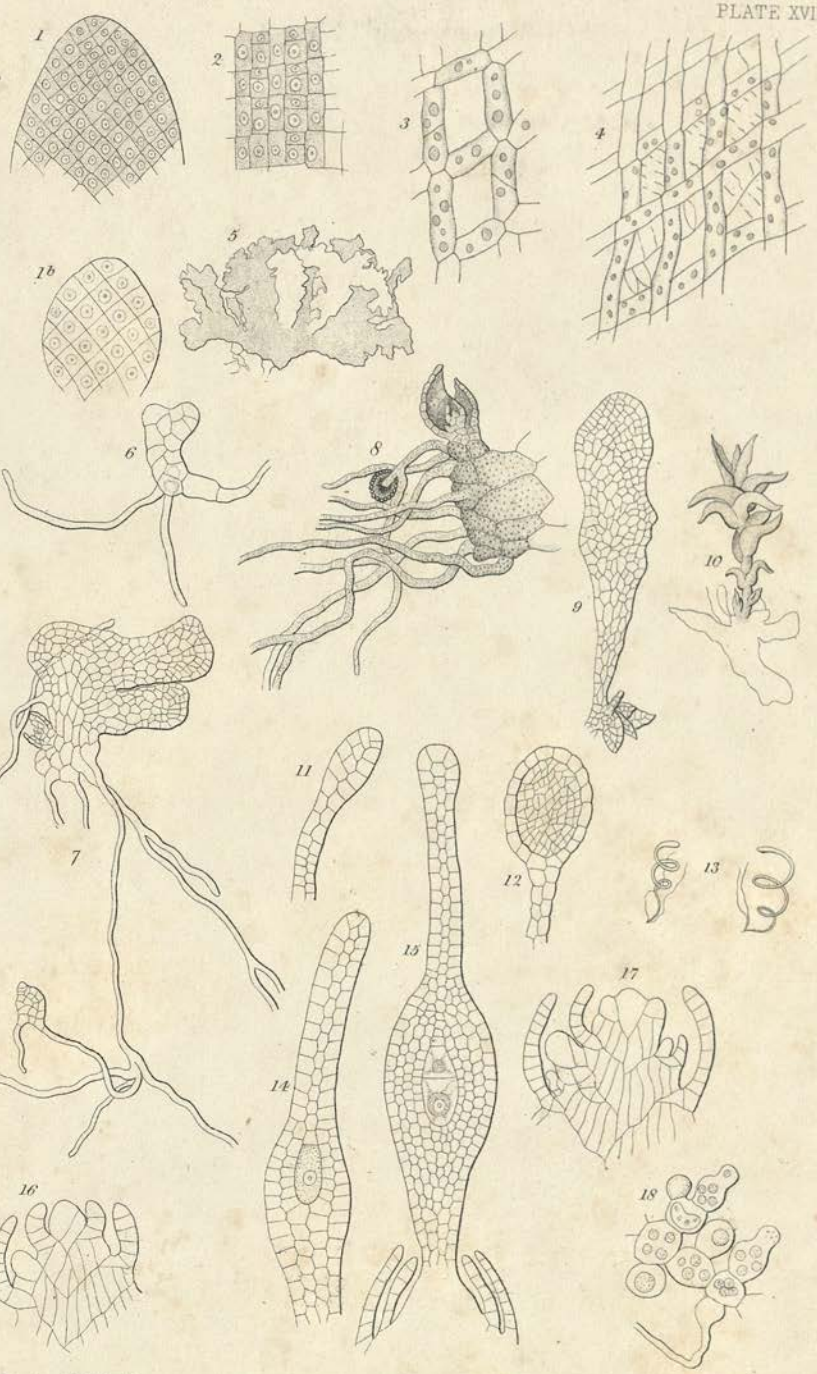

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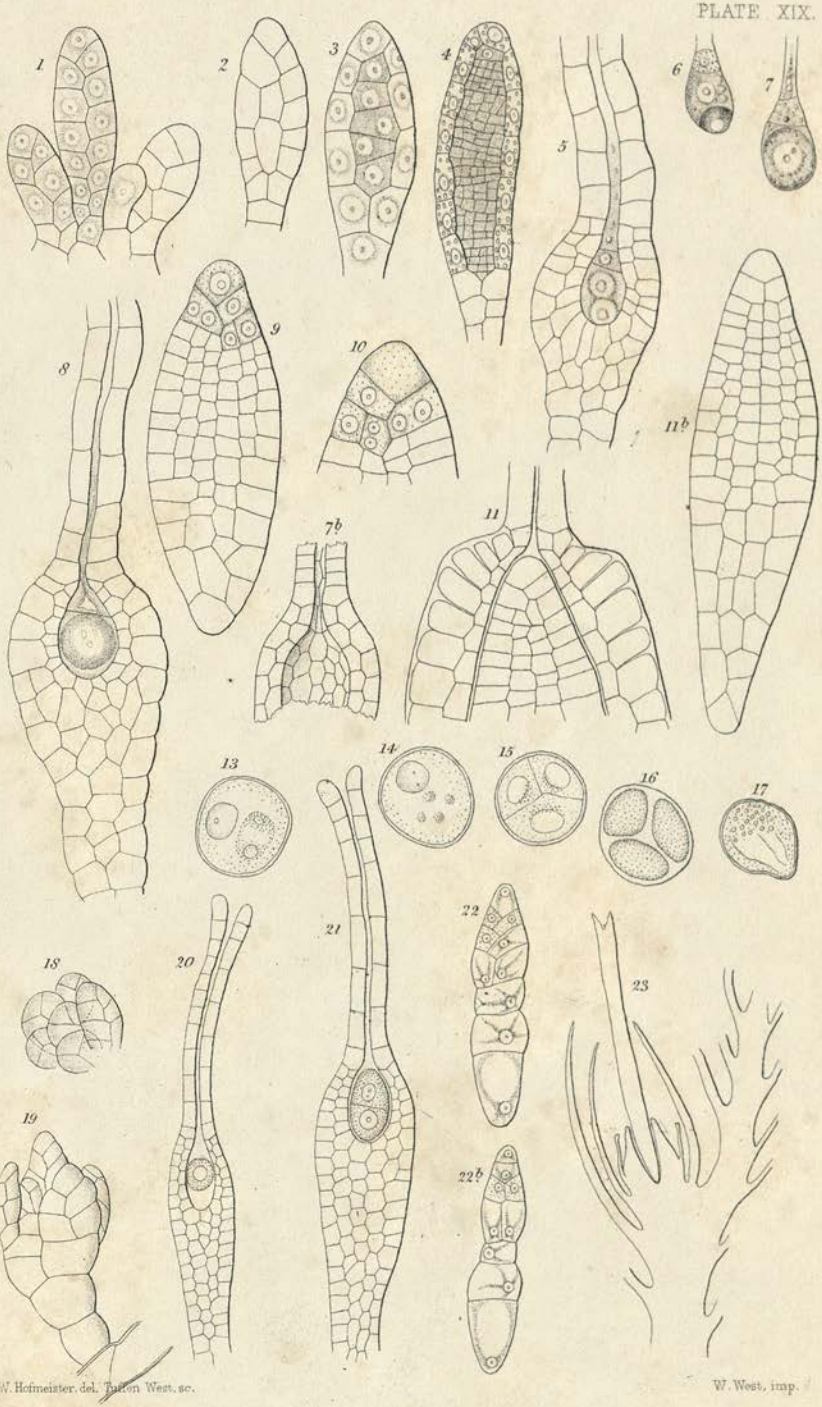

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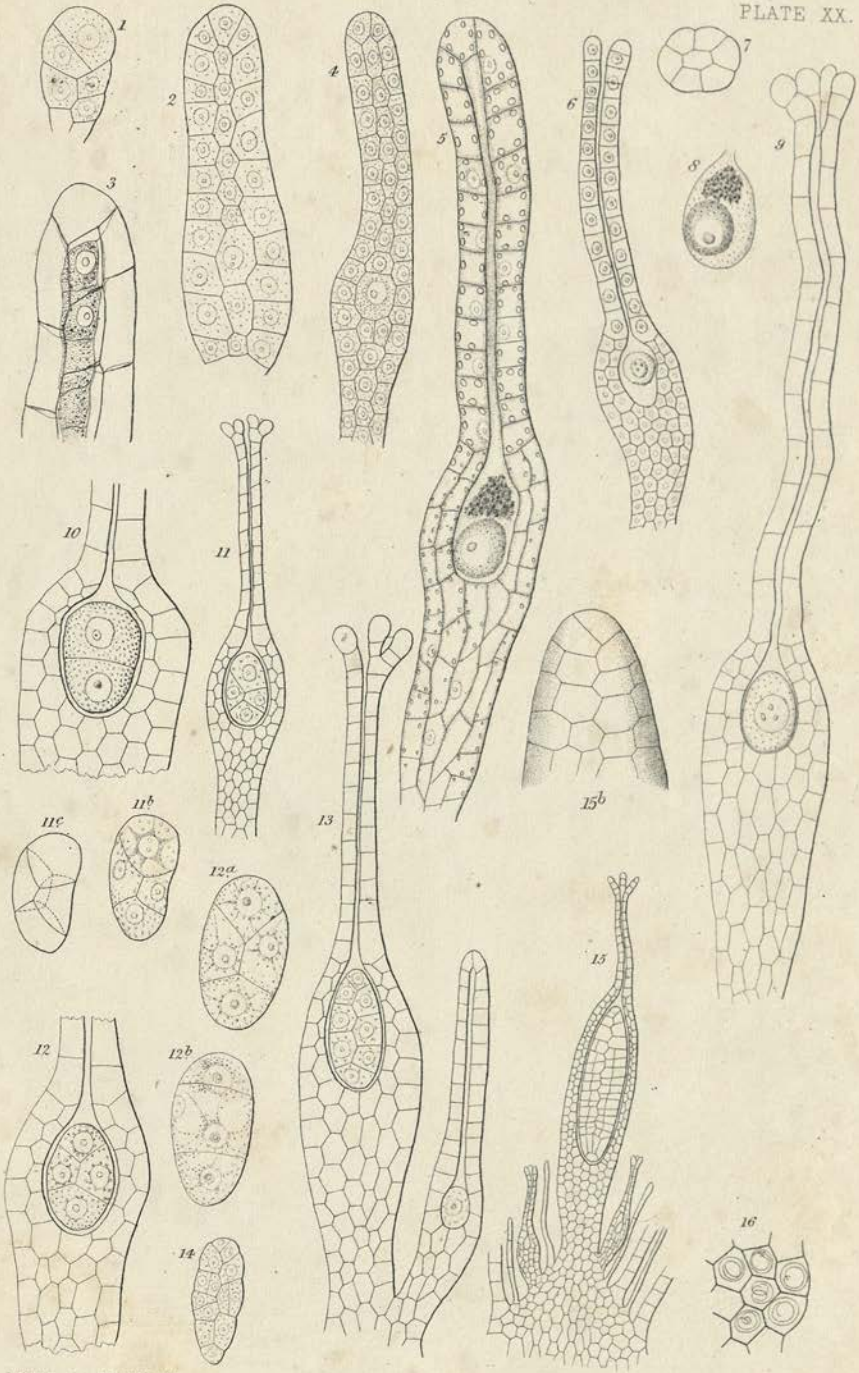

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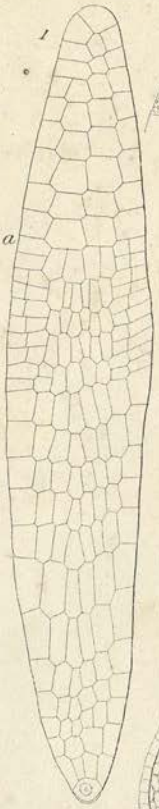

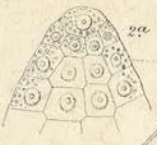

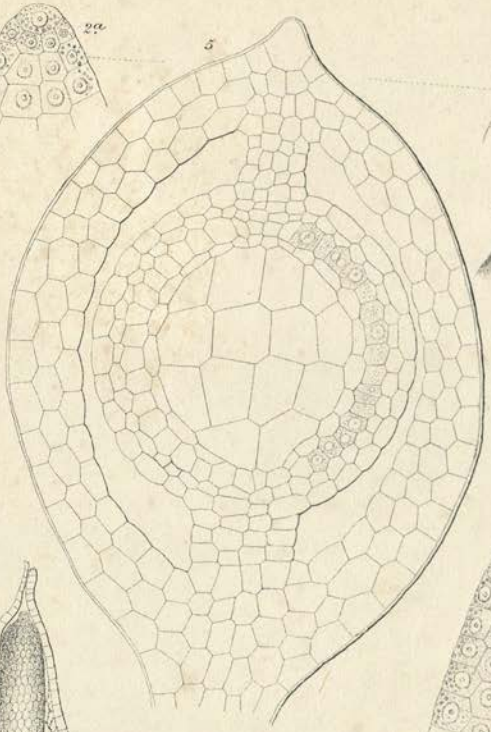

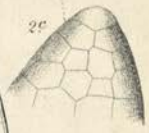

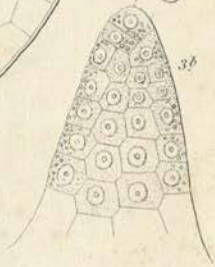

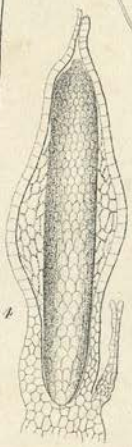

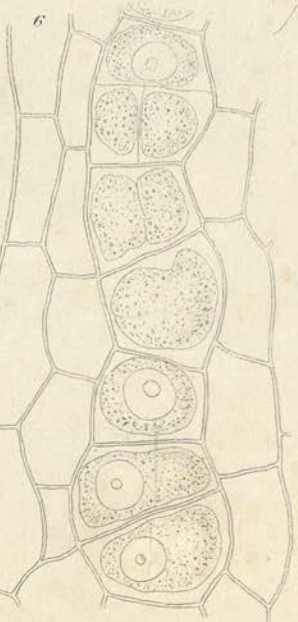

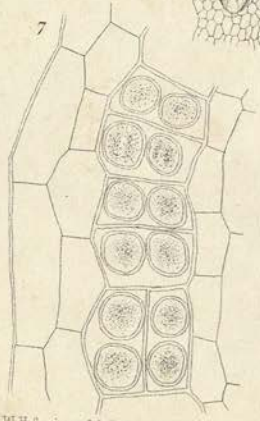

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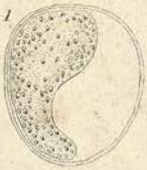
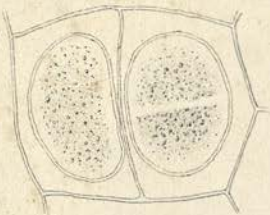
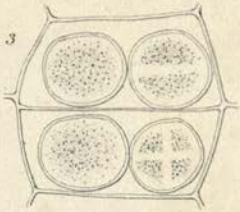
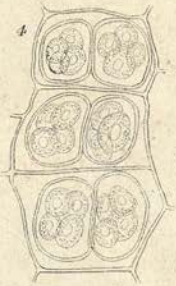
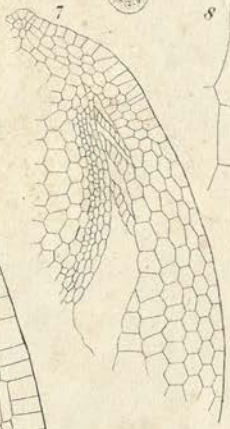
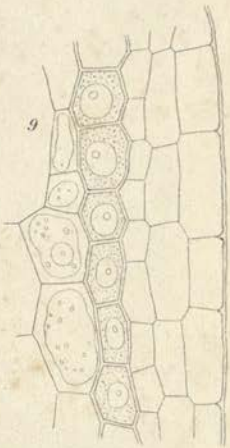


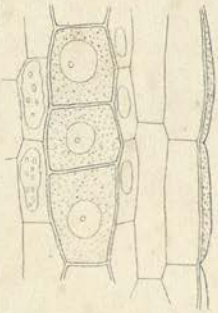


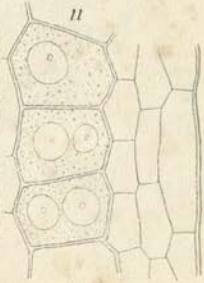


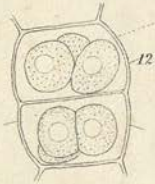


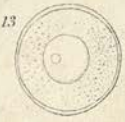


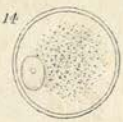


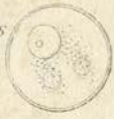


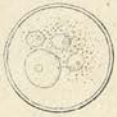






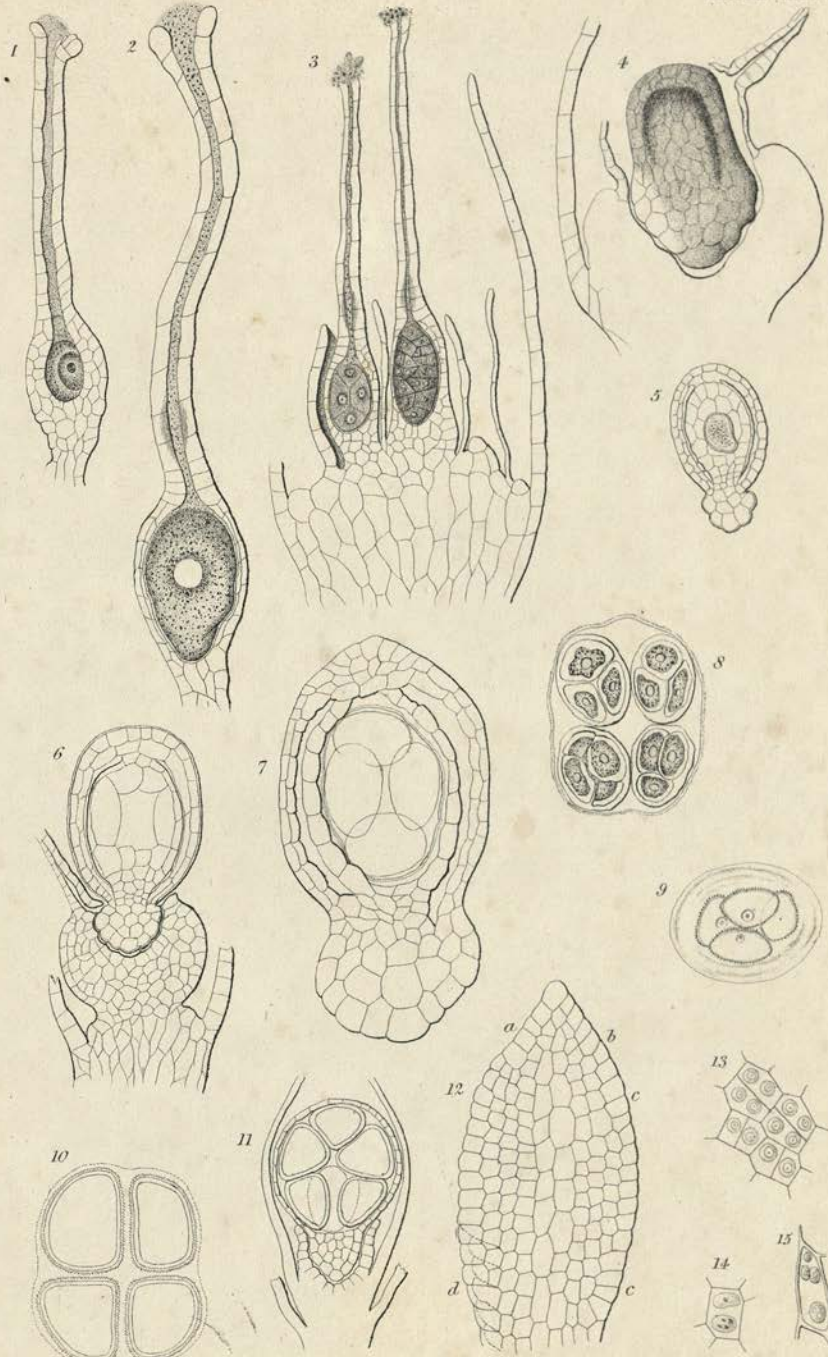






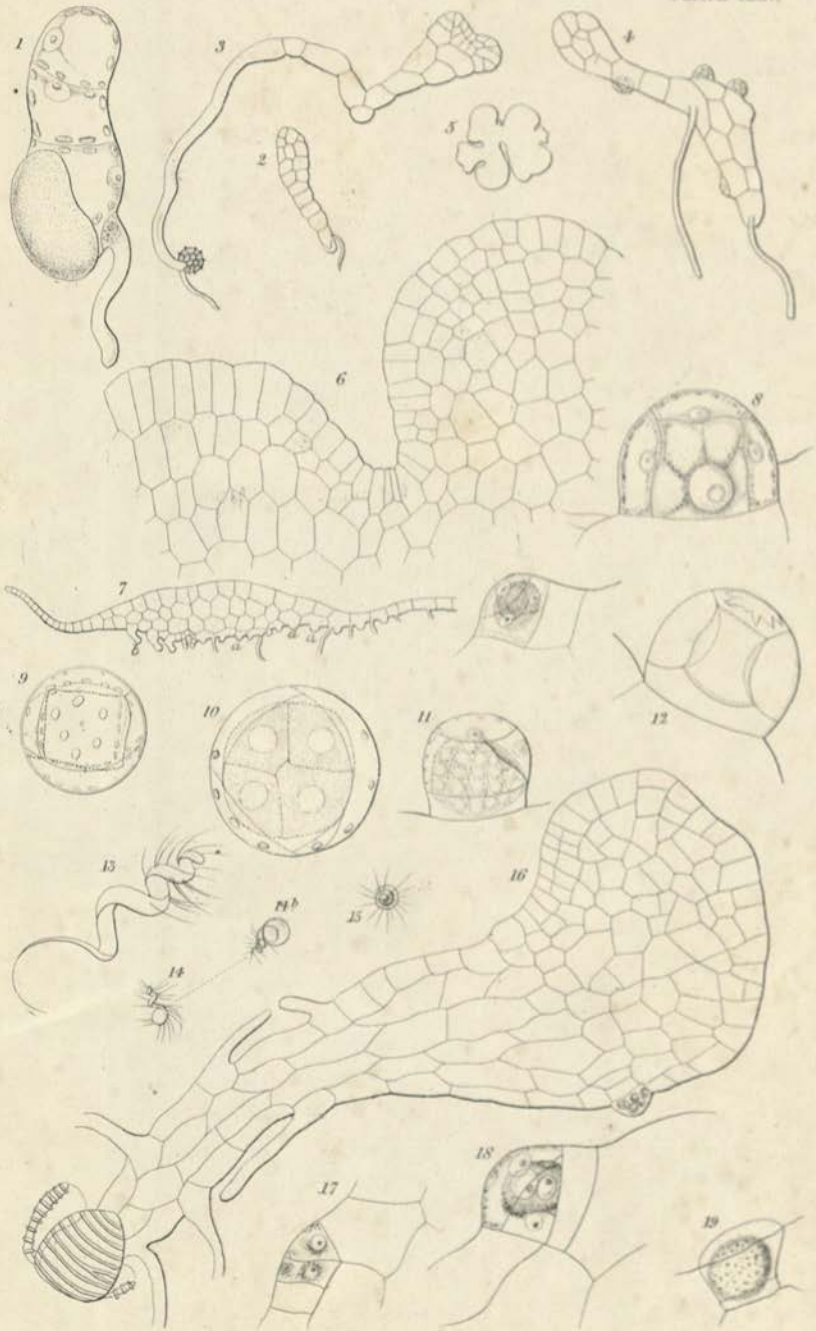
W. Hofmeister, del. Tuffen West, sc.

West, imp.



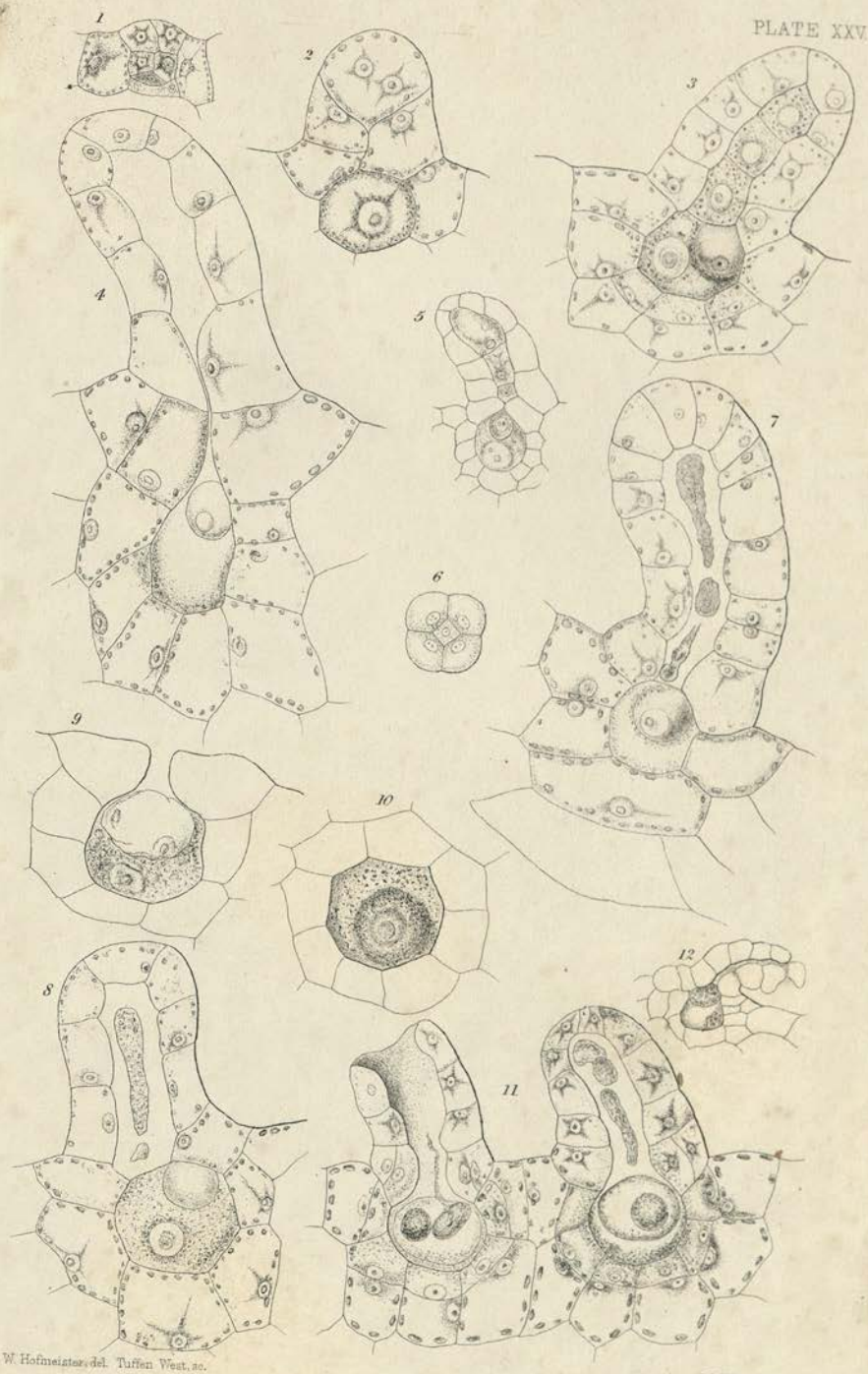
W. Hofmeister, del. Tuffen West, sc.

W. West, imp.



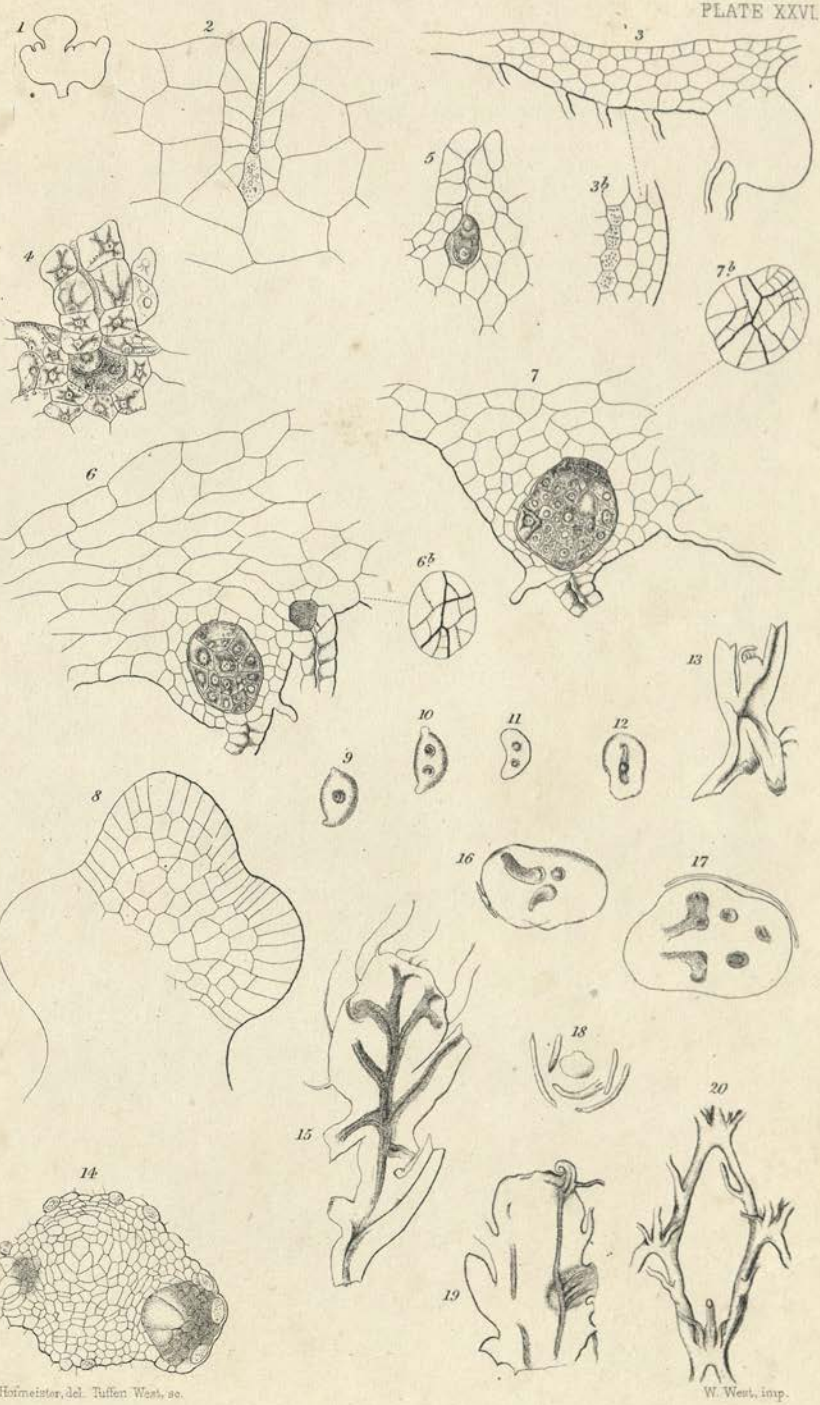
W. Hofmeister, del. Tuffen West, sc.

W. West, imp.



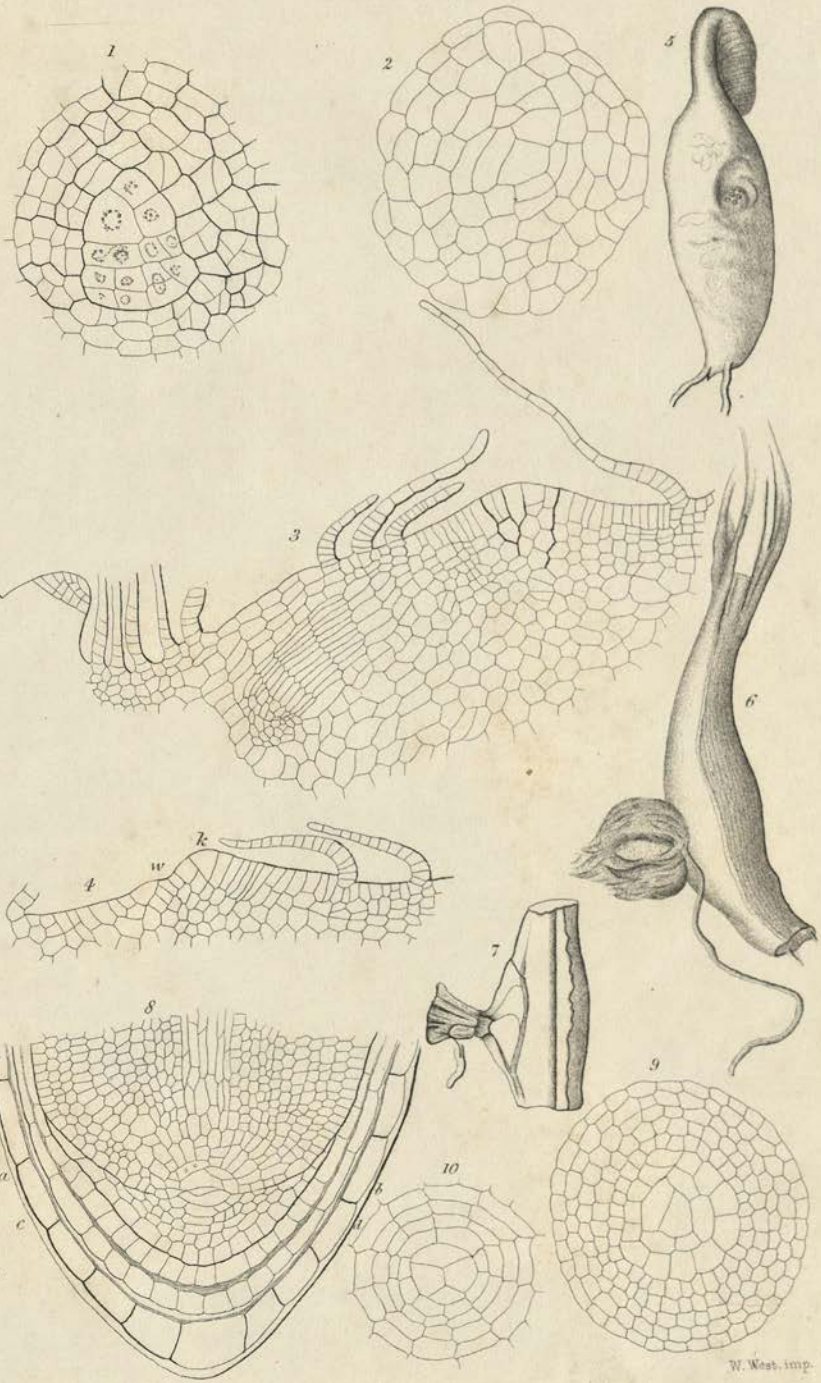
W. Hofmeister, del. Tuffen West, sc.

W. West, imp.



W. Hofmeister, del. Tuffen West, sc.

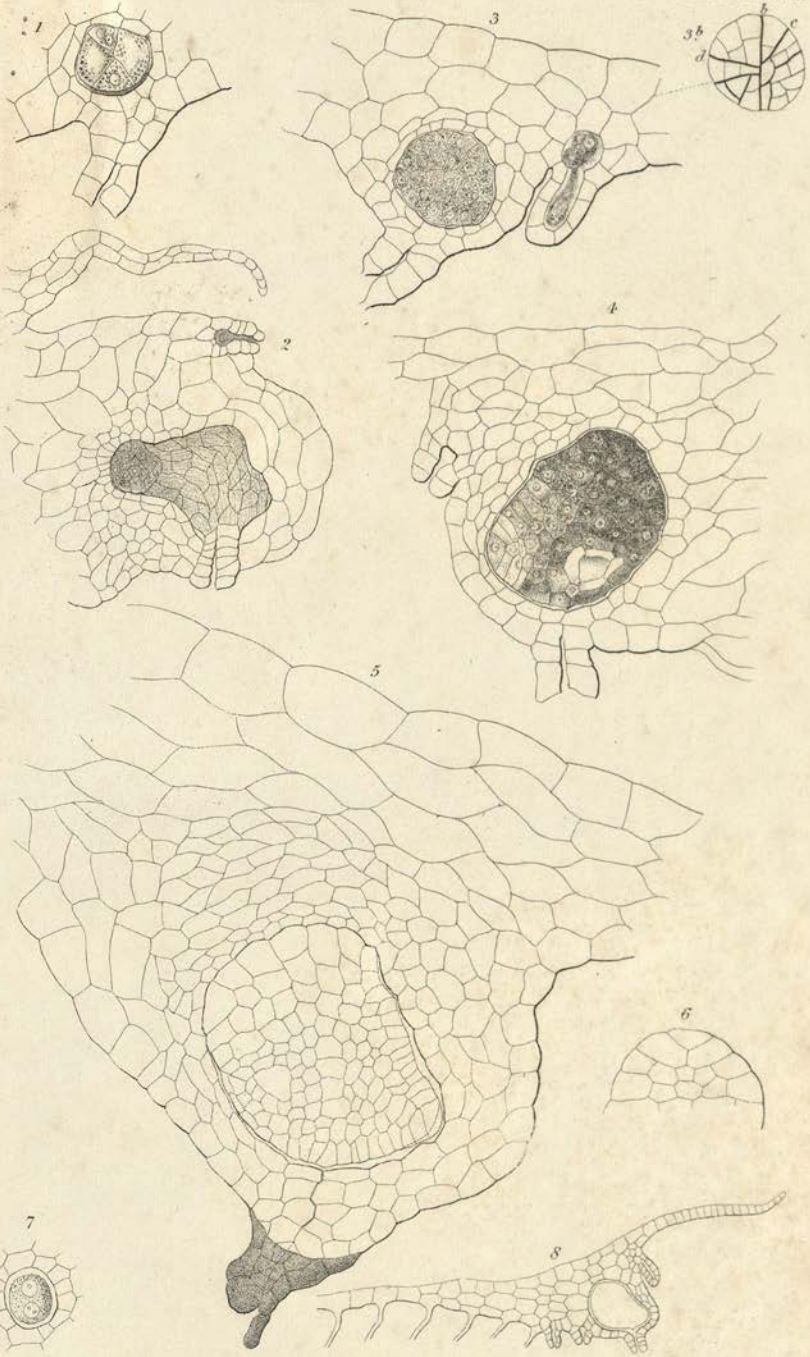
W. West, imp.



W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

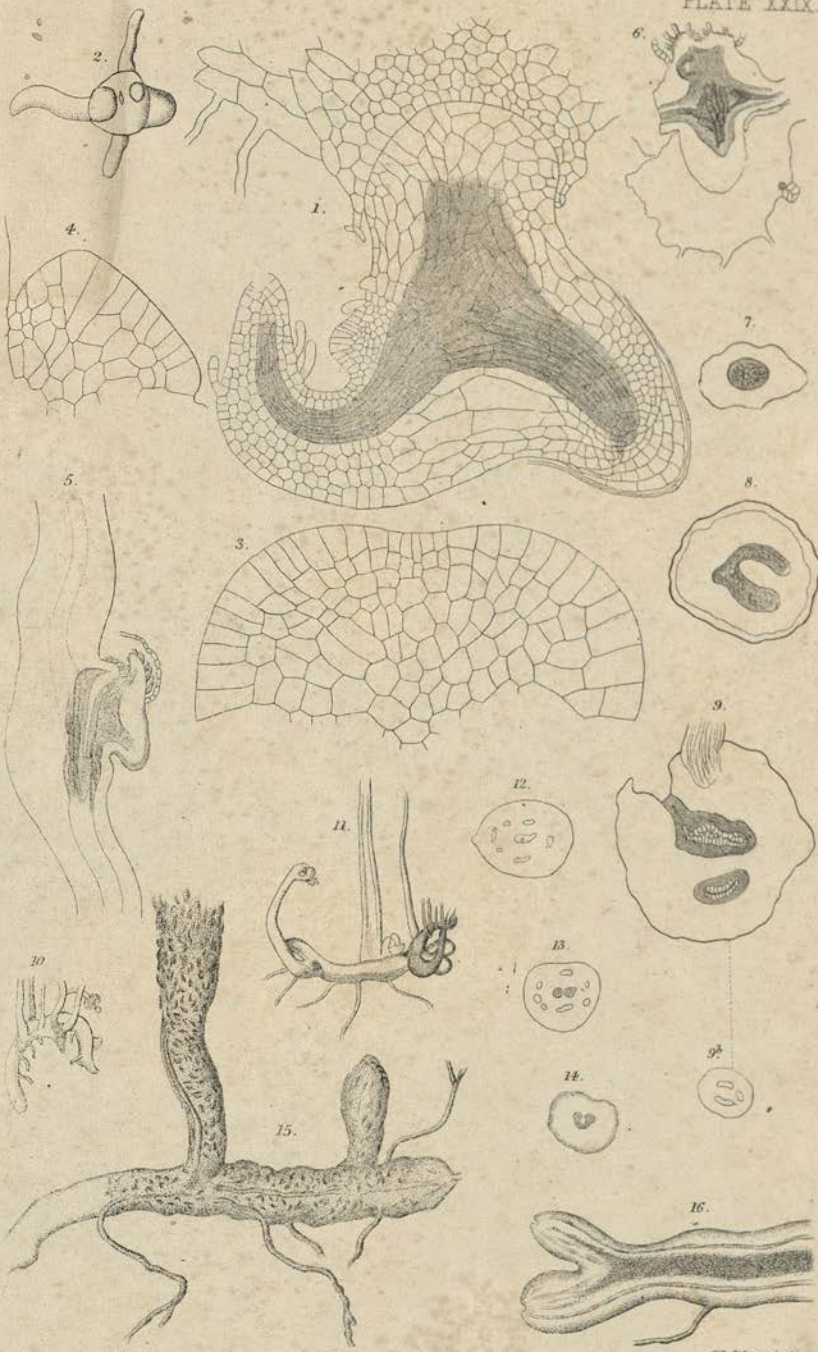
PLATE XXVIII.



W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

PLATE XXIX.



Hofmeister del. Tuffen West sc.

W. West, imp.

PLATE XXX.

1a.

1b.

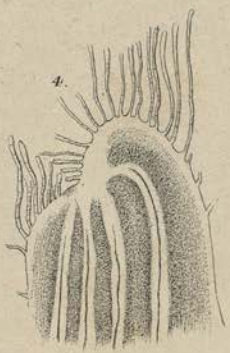
1c.

1d.

1e.

2.

3.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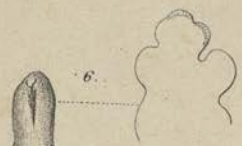
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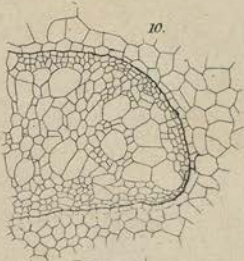
7.

8.

9.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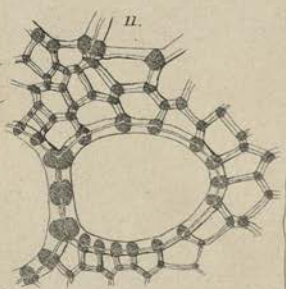
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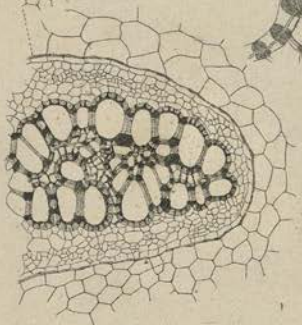
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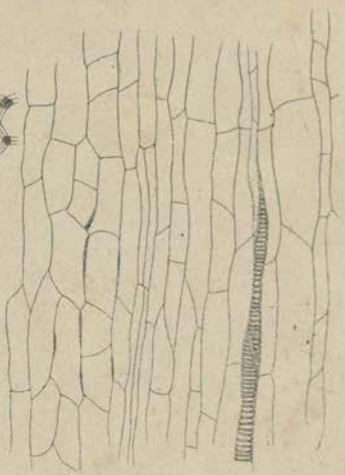
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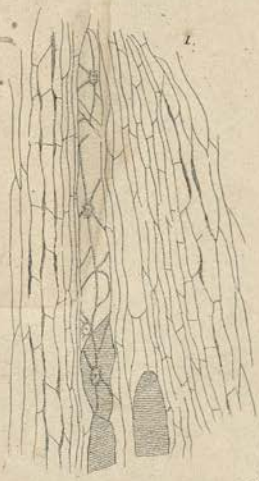
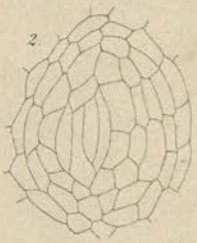
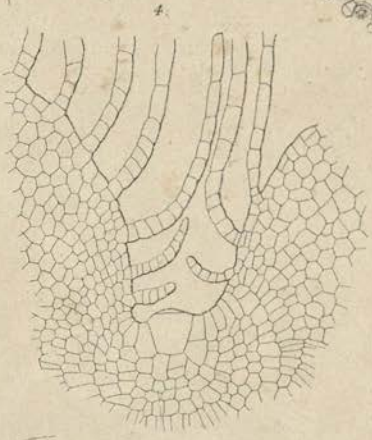
W. Hofmeister, del. Tuffen West, sc.

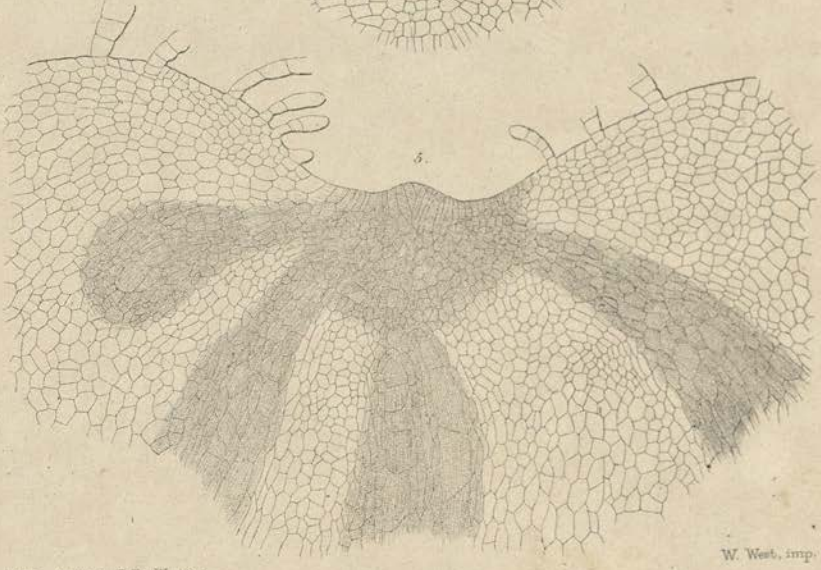
W. West, imp.

PLATE XXXI.









W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

PLATE XXXII.

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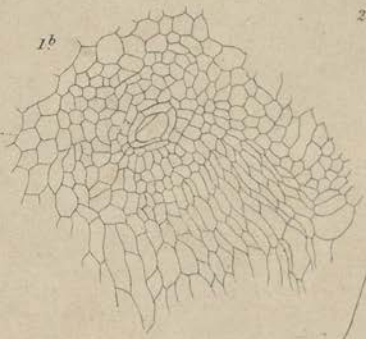
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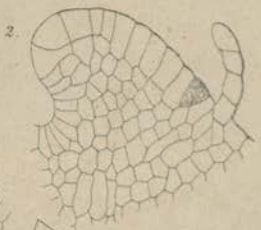
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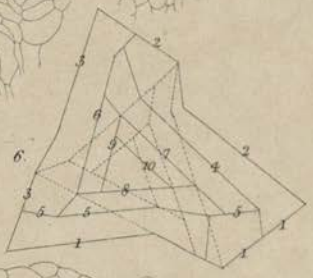
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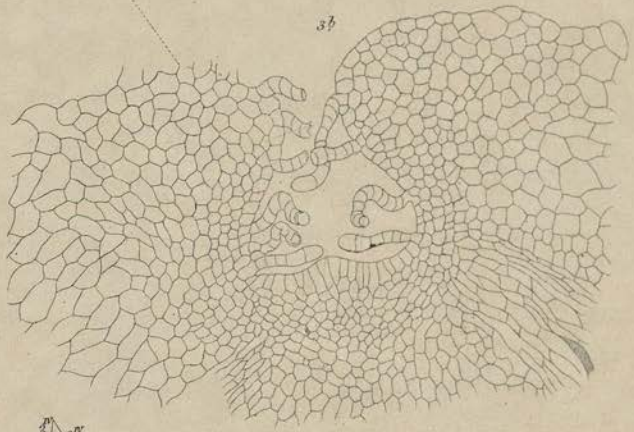
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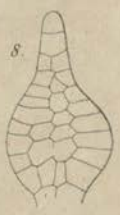
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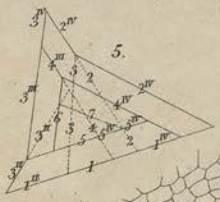
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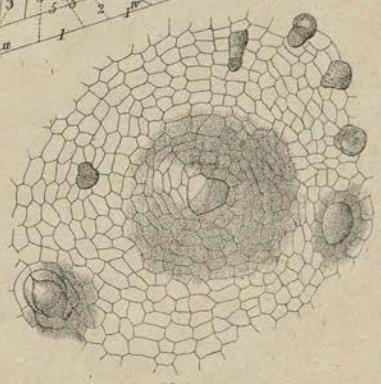
4

10.

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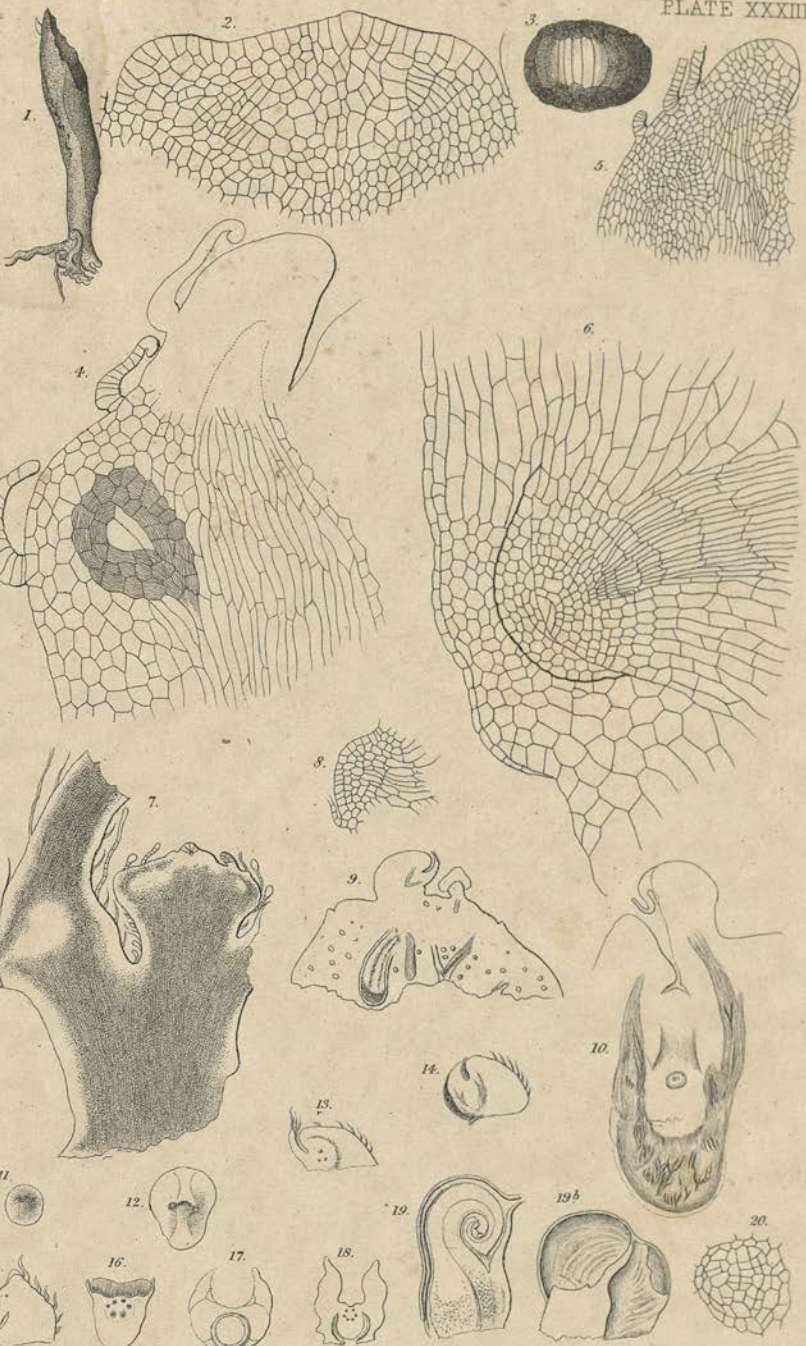
14.

W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

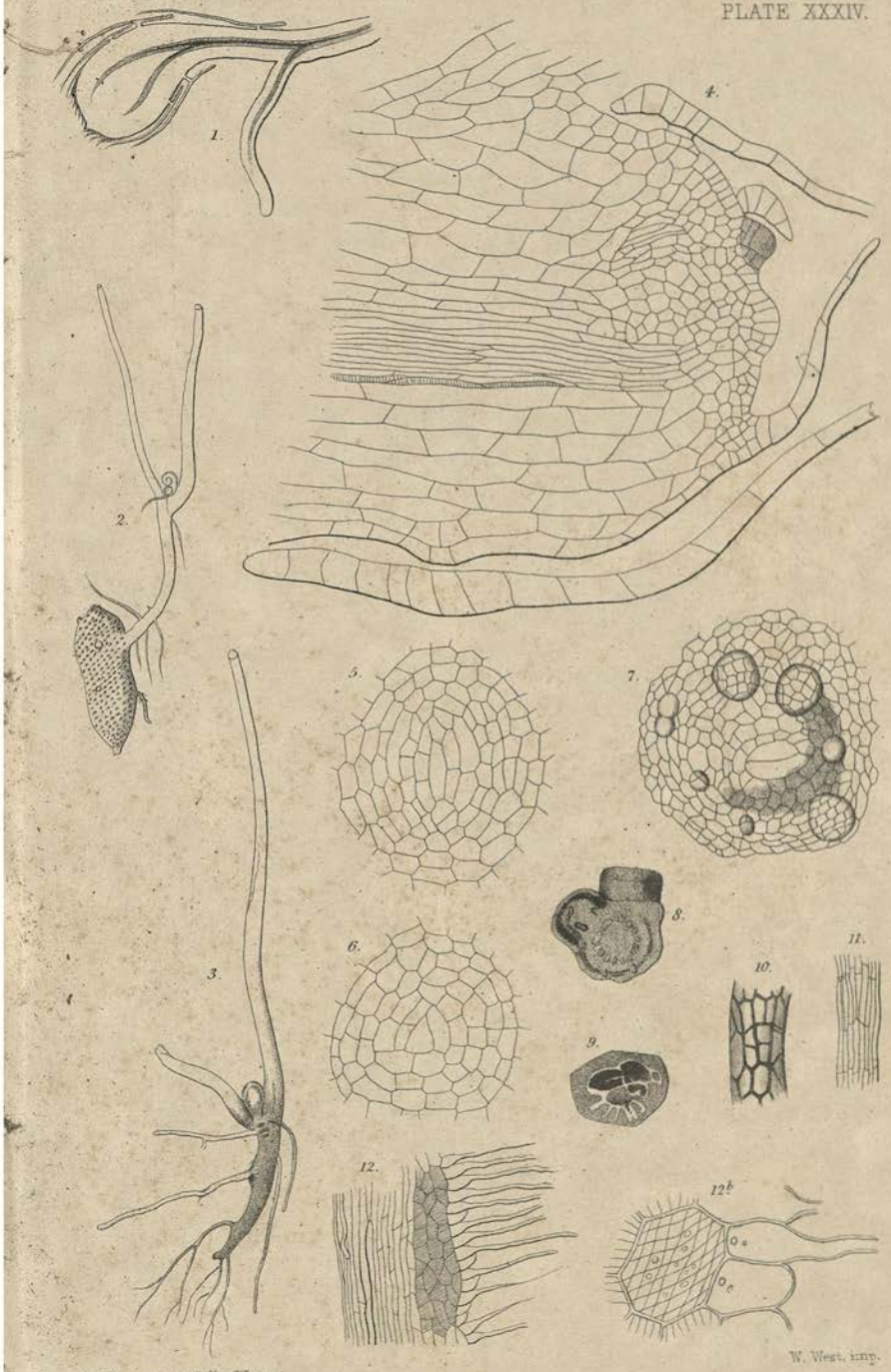
PLATE XXXIII



W. Hofmeister, del. Ruthin. West, sc.

W. West, imp.

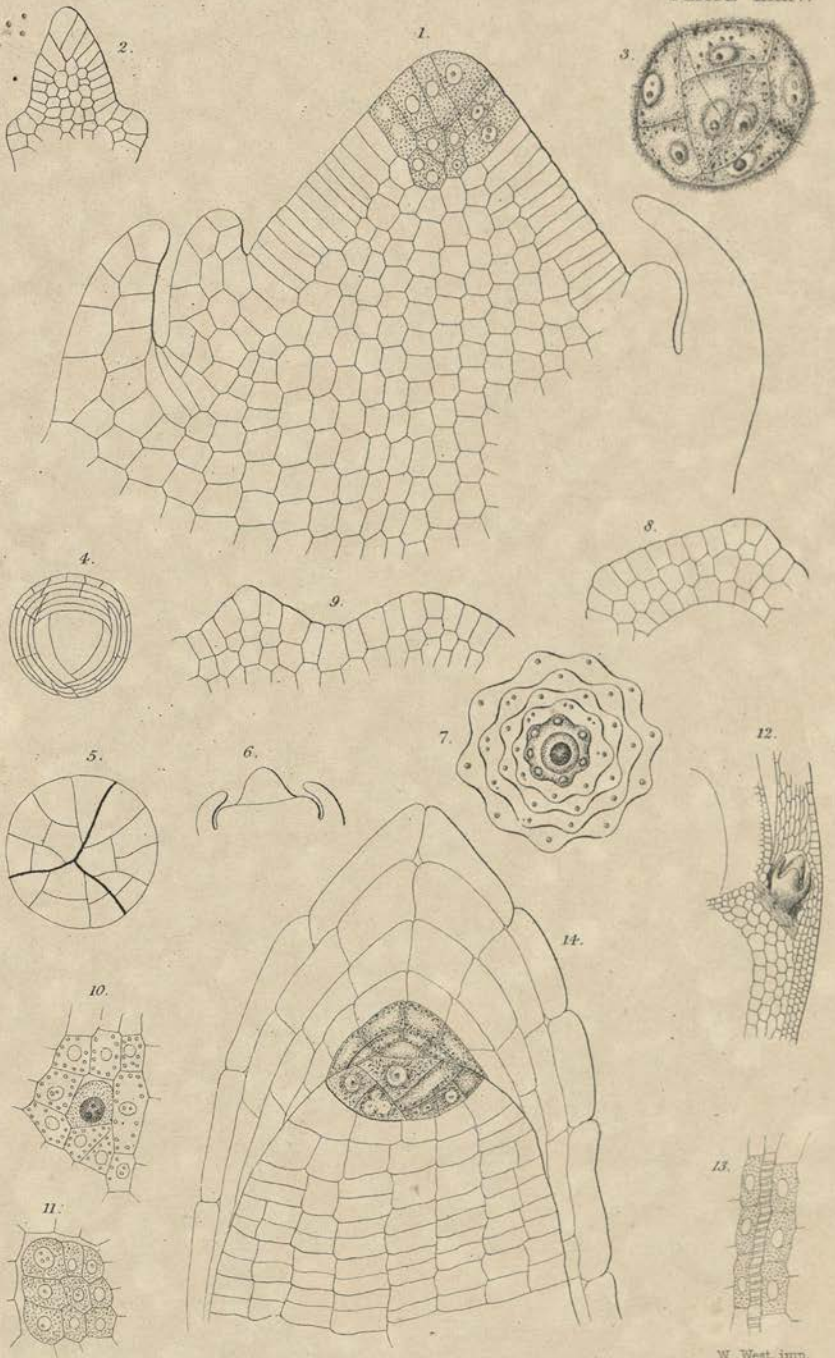
PLATE XXXIV.



W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

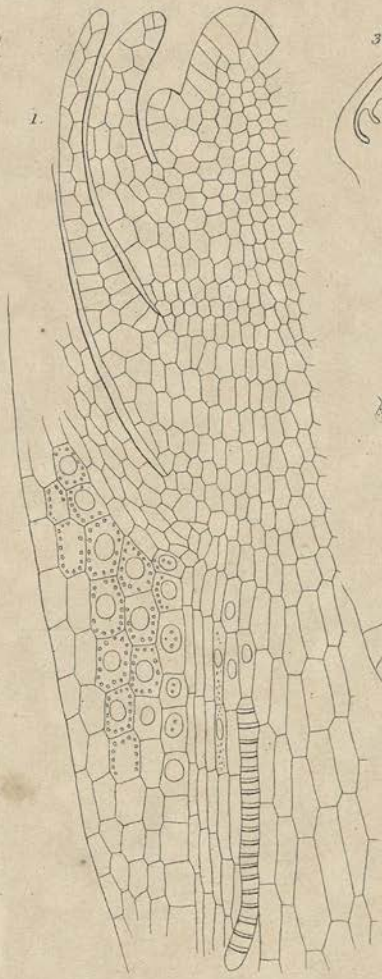
PLATE XXXV.

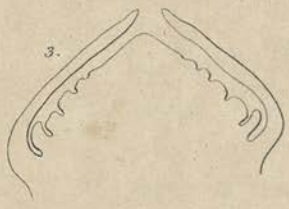


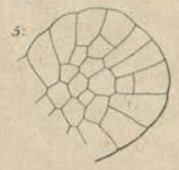
W. Hofmeister, del. Tuffen West, sc.

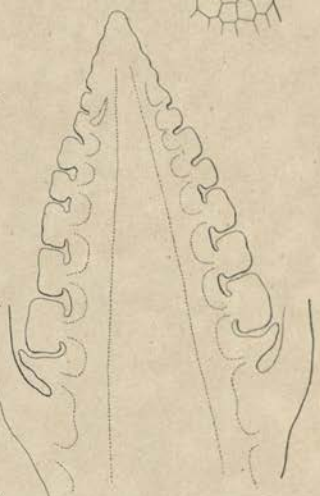
W. West, imp.

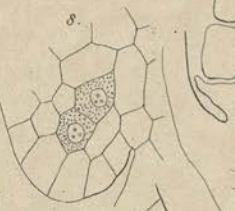
PLATE XXXVI.

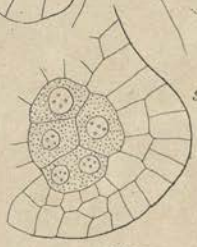


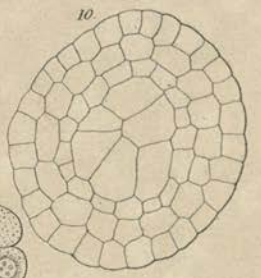


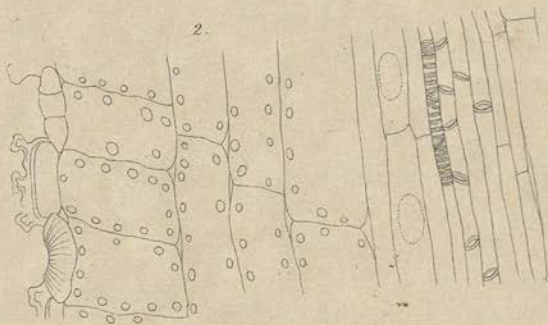


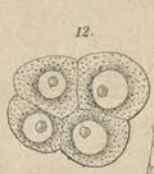


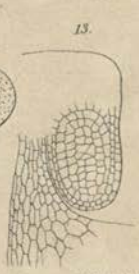






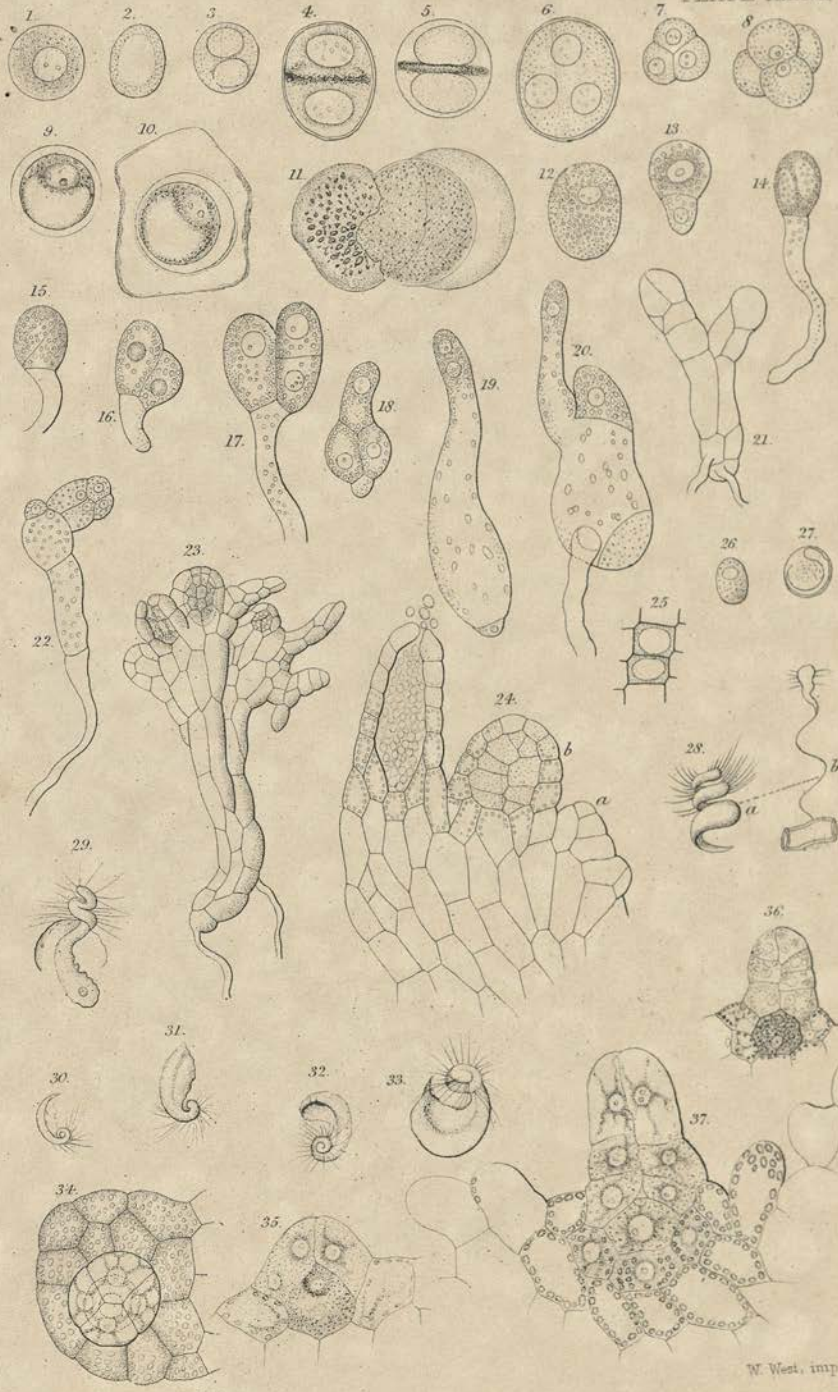






W. Hofmeister, del. Tuffen West, sc.

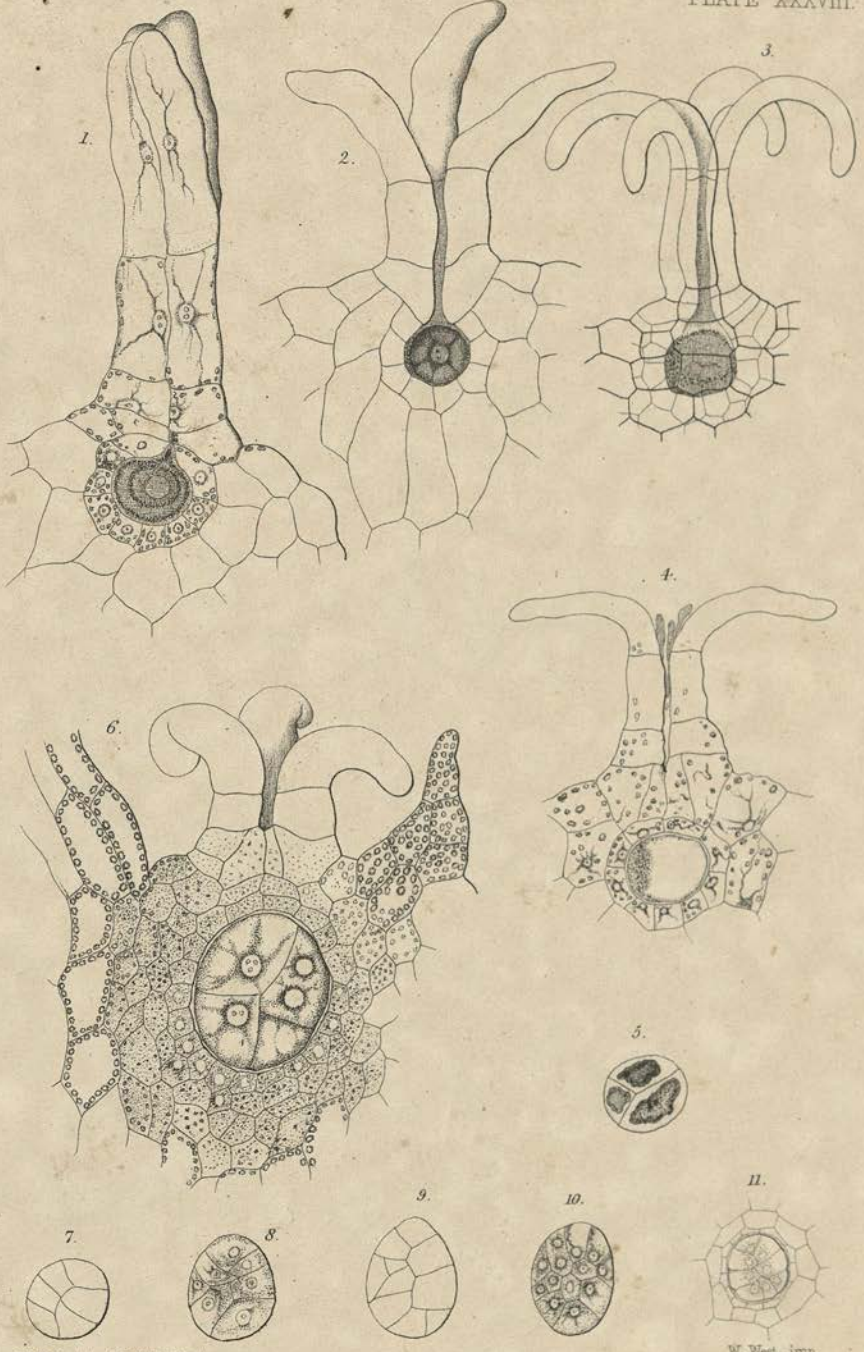
W. West, imp.



W. Hofmeister. del. Tuffen West, sc.

W. West, imp.

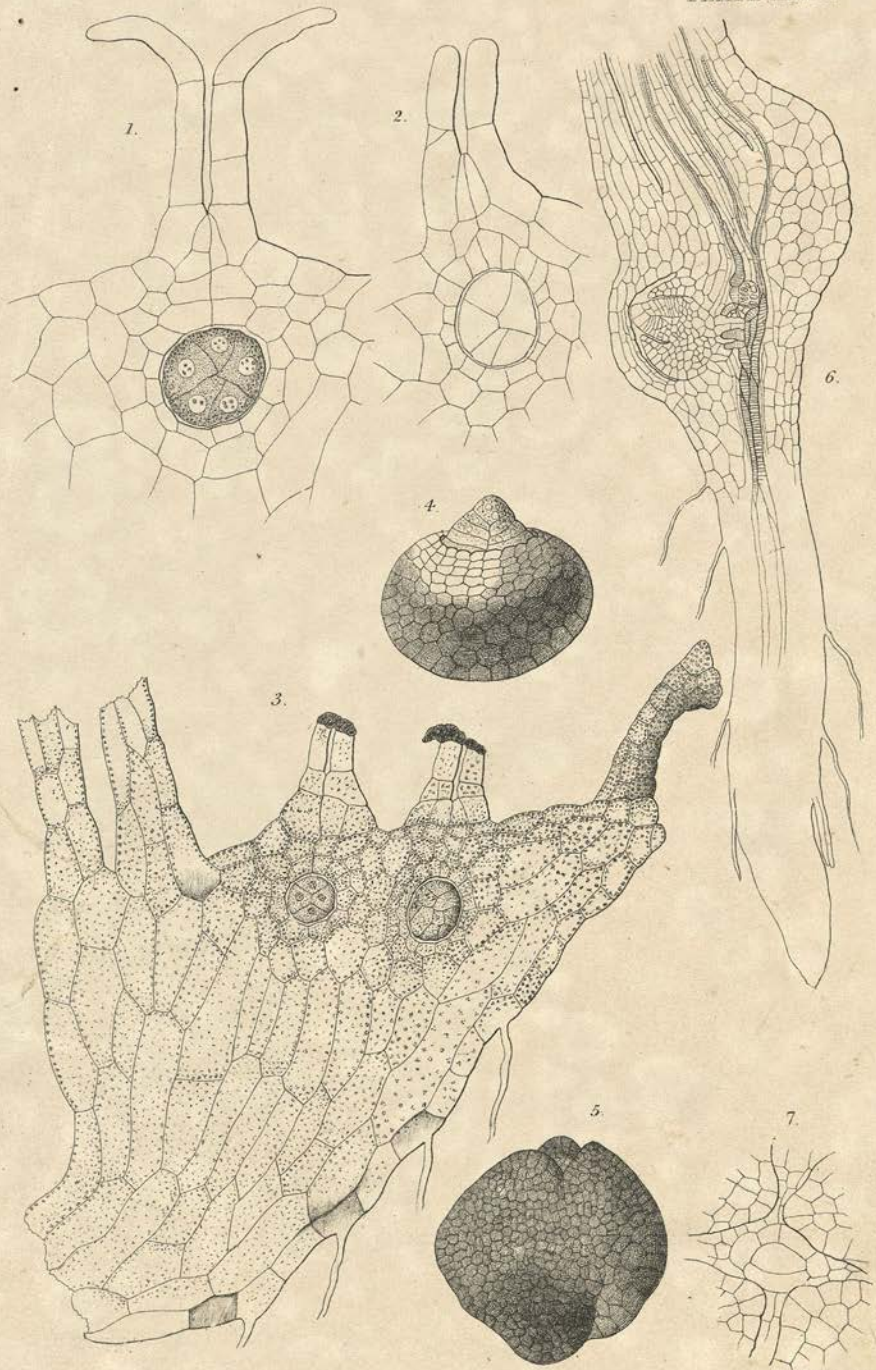
PLATE XXXVIII.



W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

PLATE XXXIX.

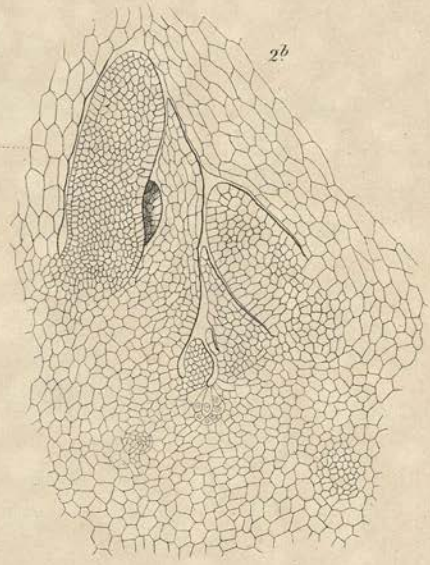


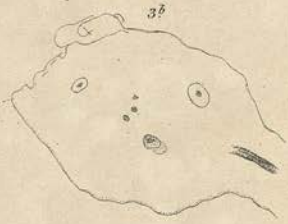
W. Hofmeister, del. Tuffen West, sc.

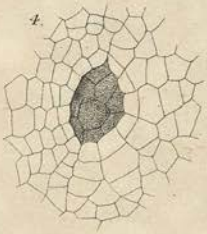
W. West, imp.

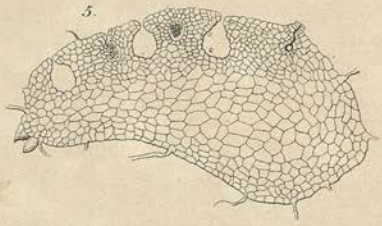
W. Hofmeister, del. Tuffen West, sc.

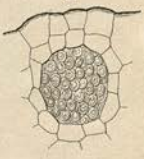
W. West, imp.

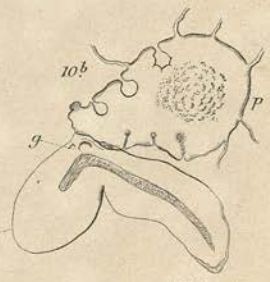






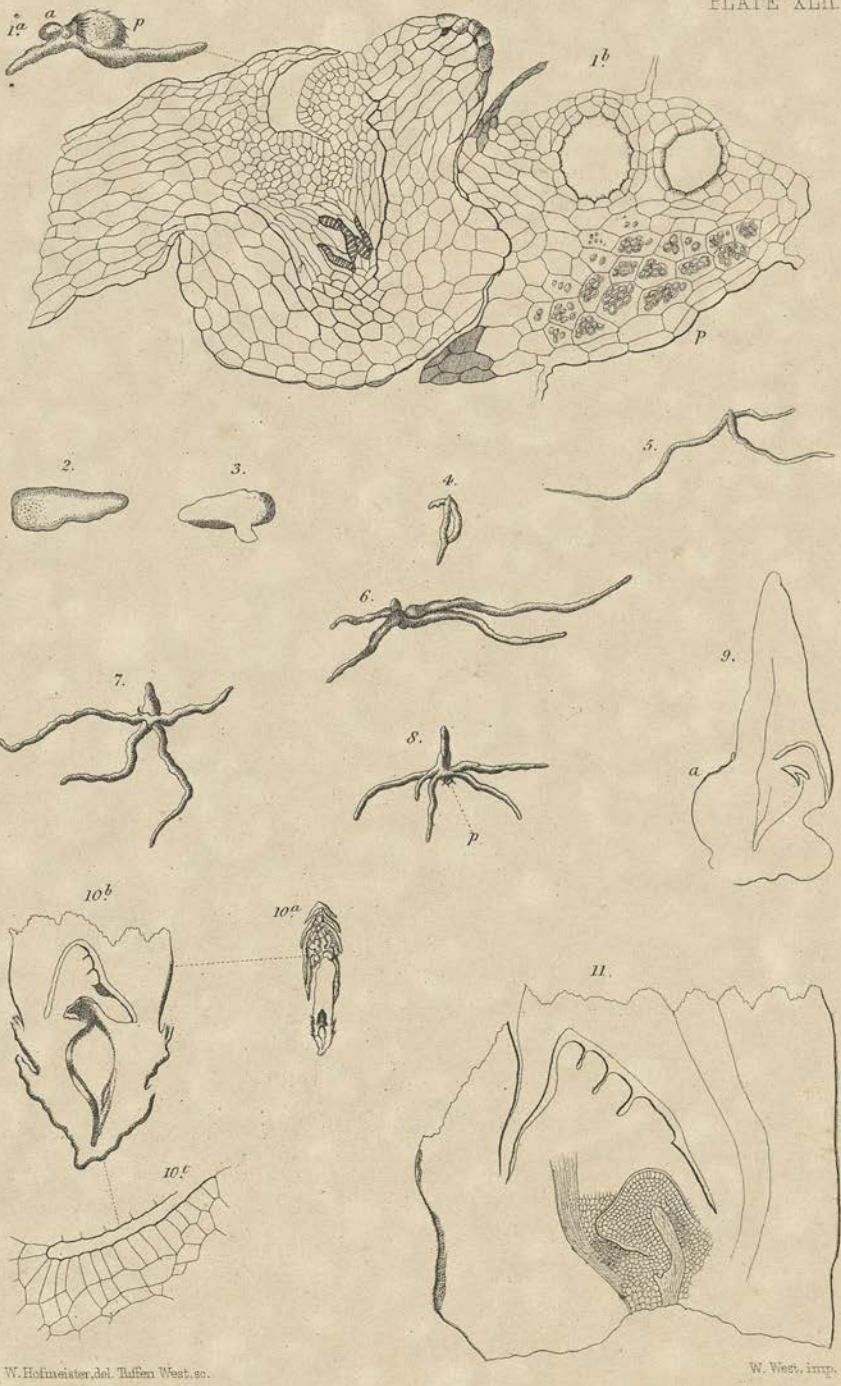






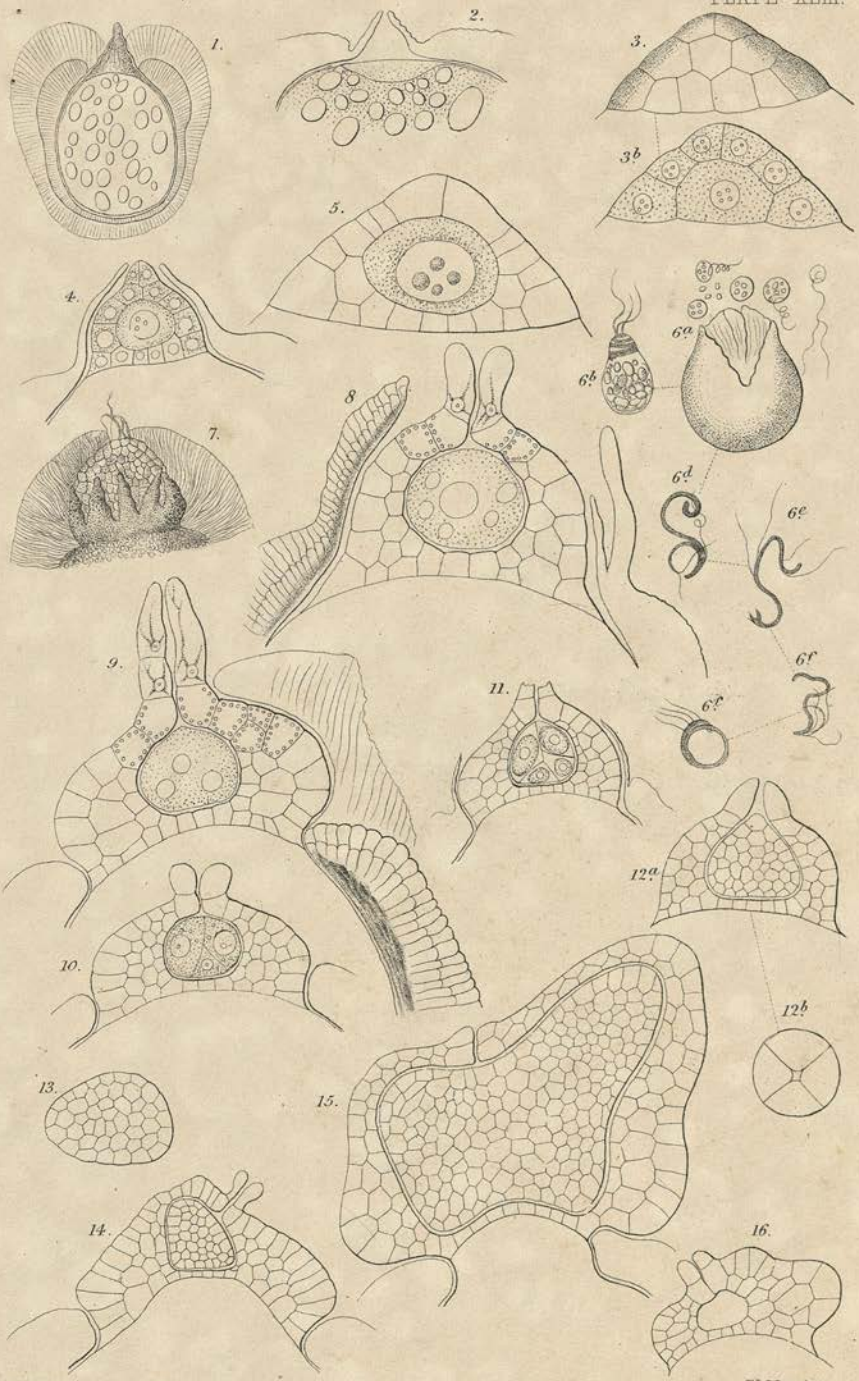
W. Hoffmeister, del. Tuffen West, sc.

W. West, imp.



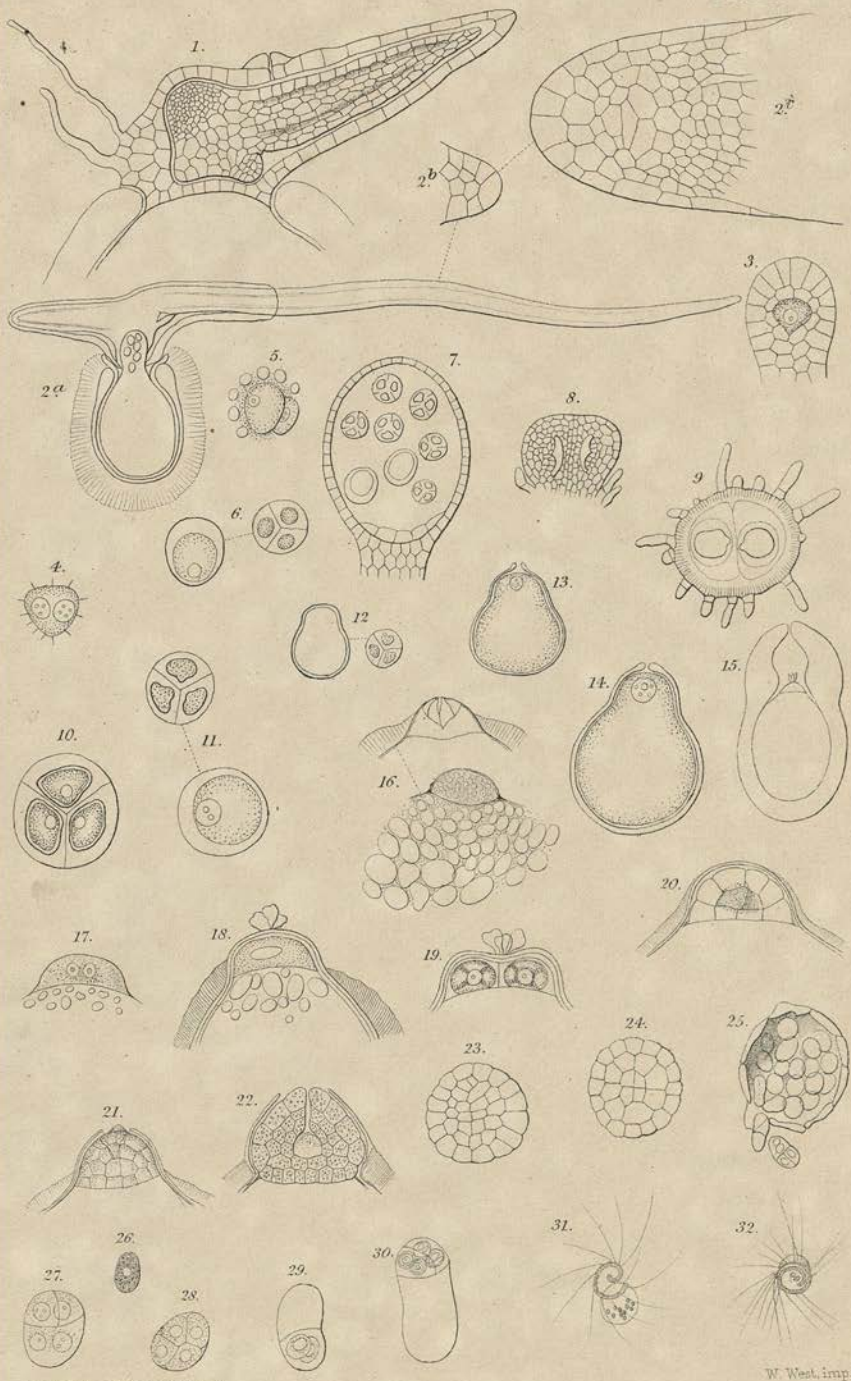
W. Hofmeister, del. Tuffen West, sc.

W. West, imp.



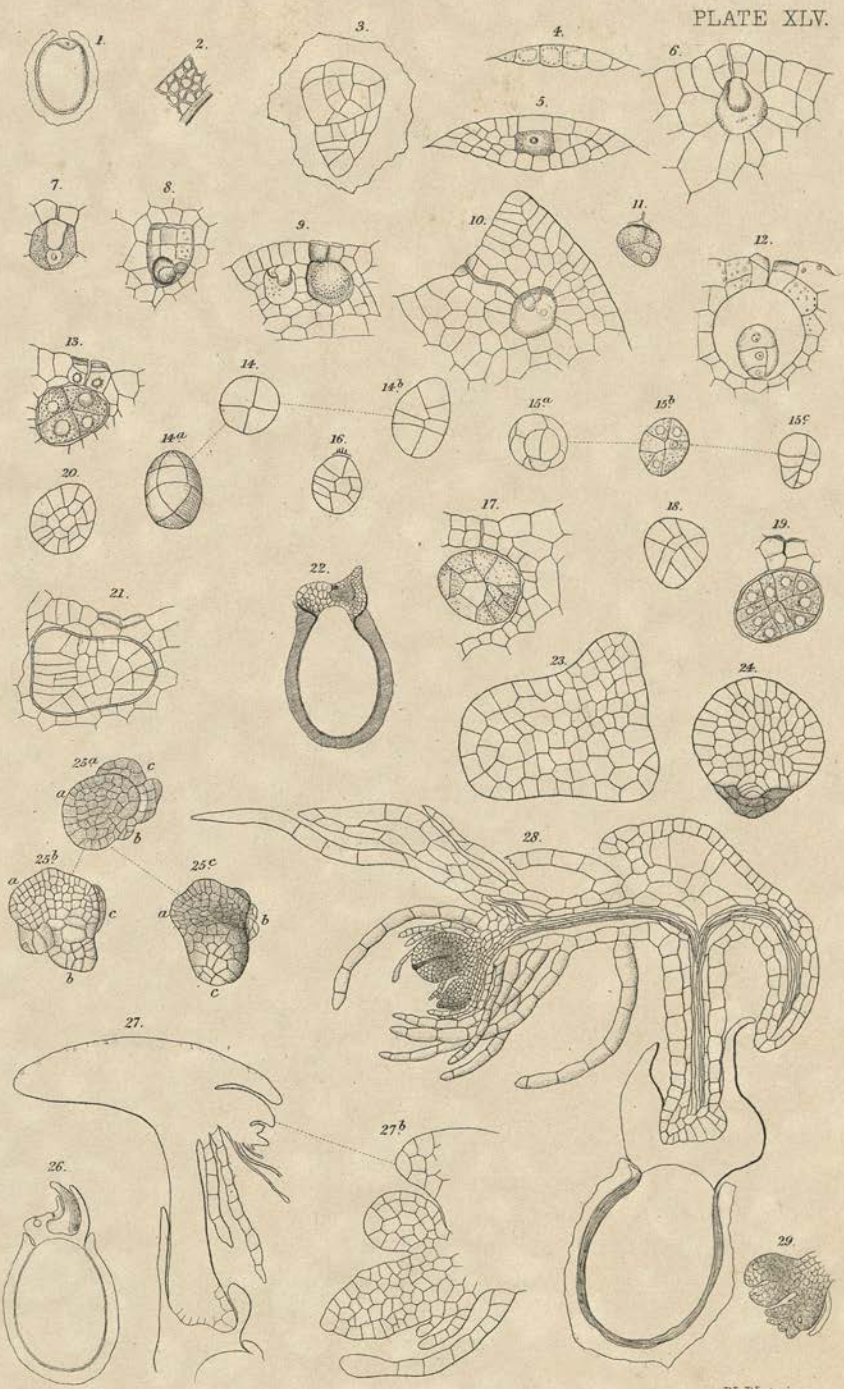
W. Hofmeister, del. Tuffen West, sc.

W. West, imp.



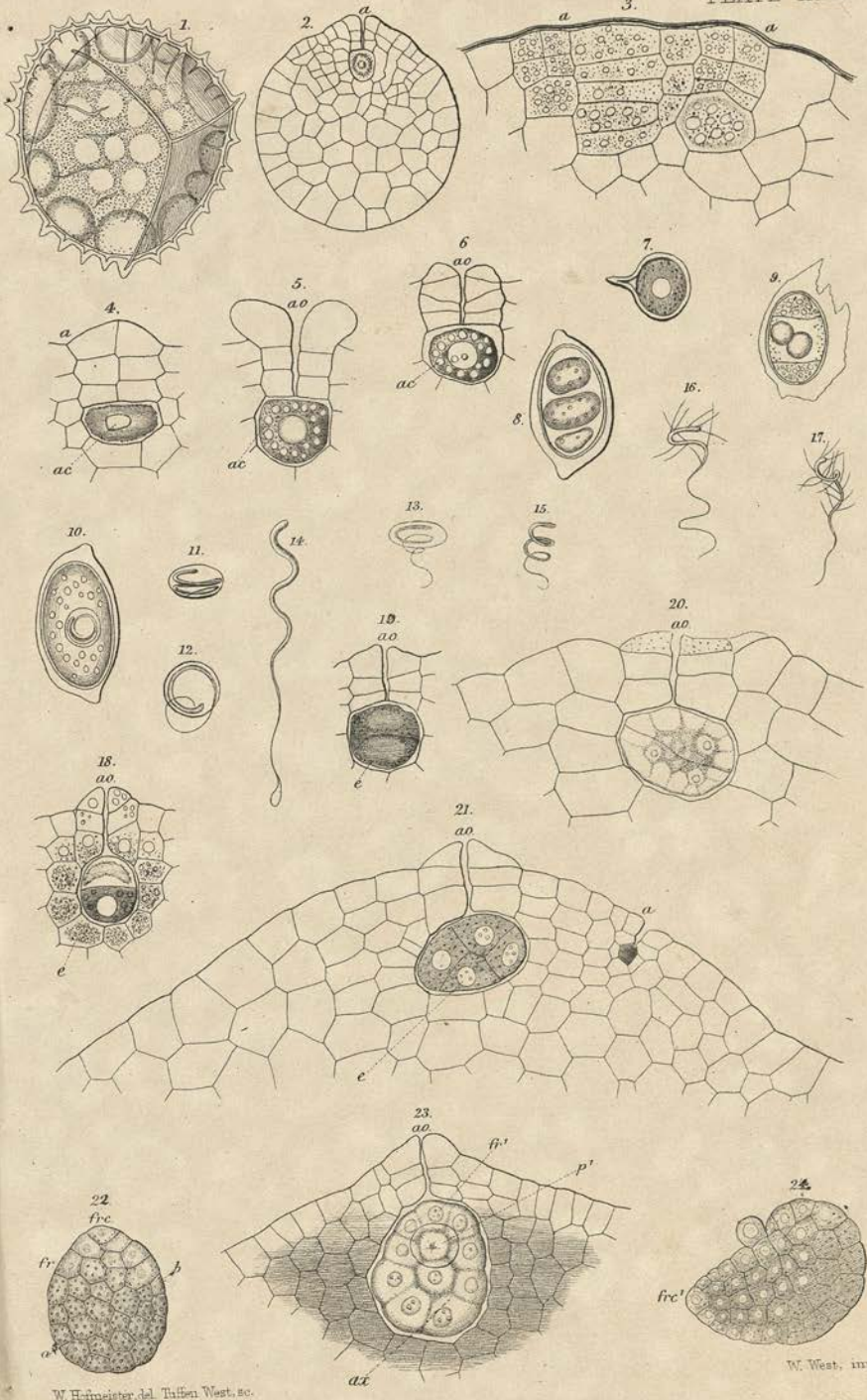
W.Hofmeister, del. Tuffen West, sc.

W. West, imp.



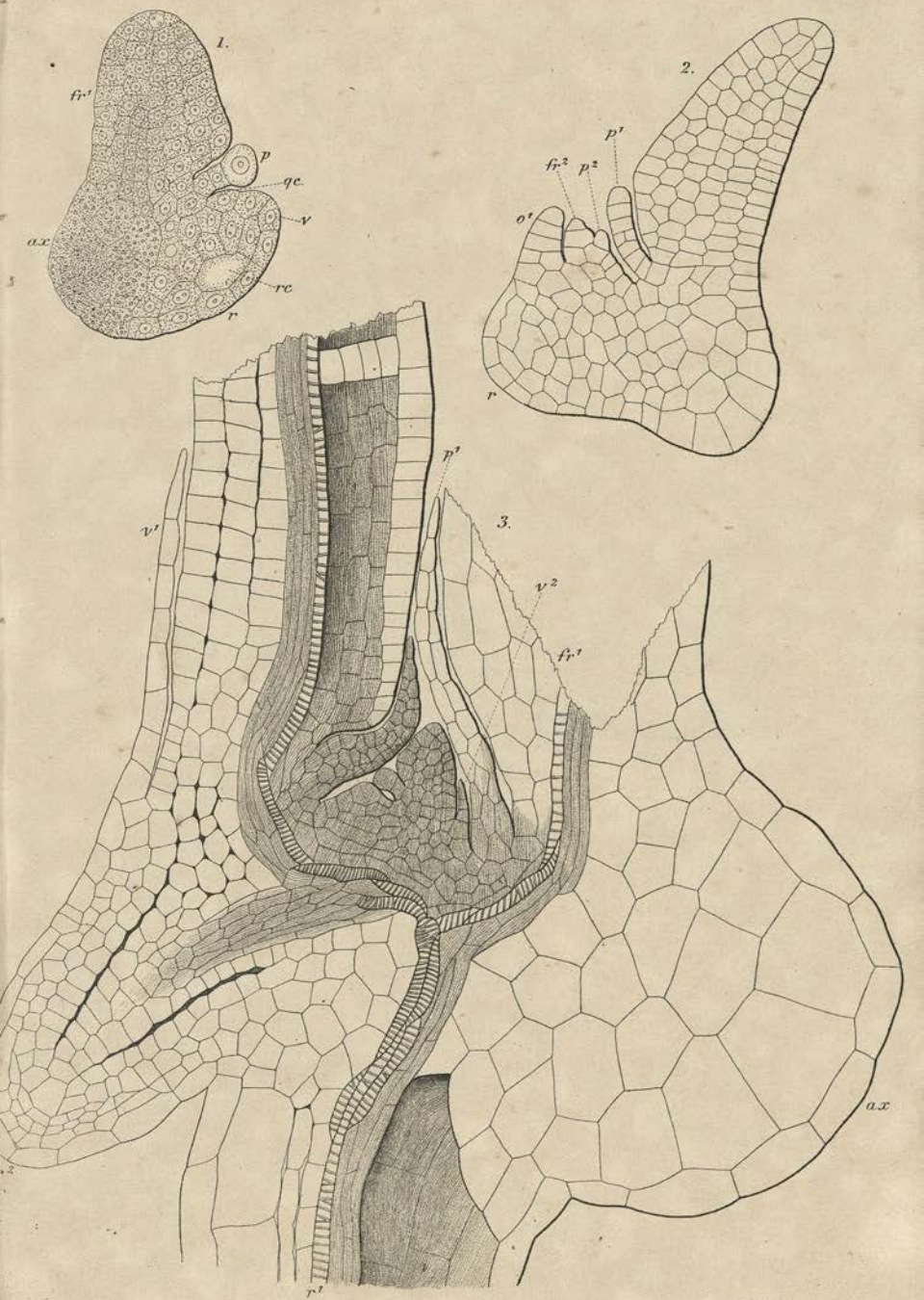
W. Hofmeister del. Tuffen West, sc.

W. West, imp.



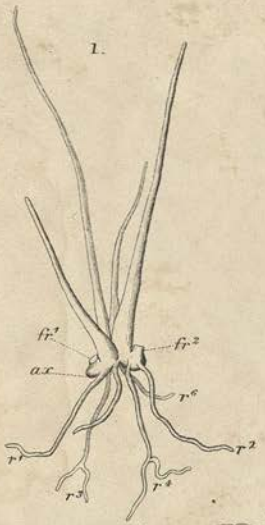
W. Hofmeister, del. Taffen West, sc.

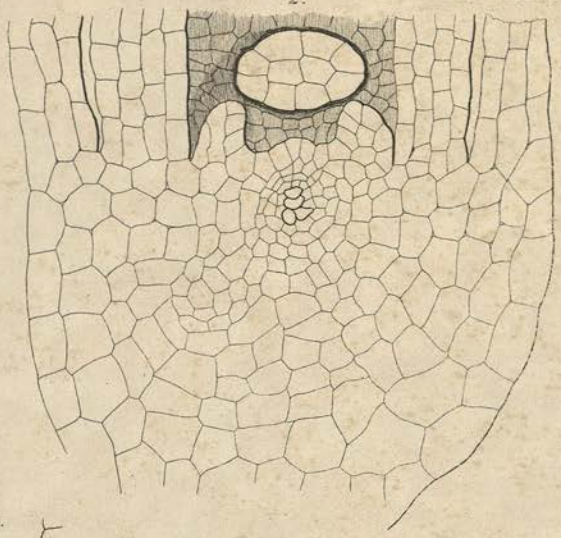
W. West, imp.

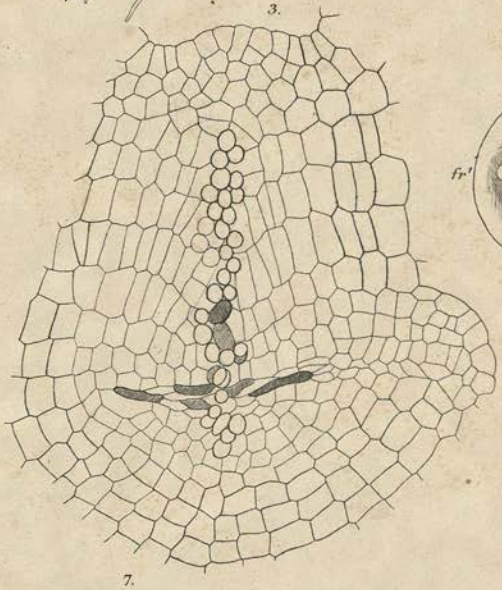


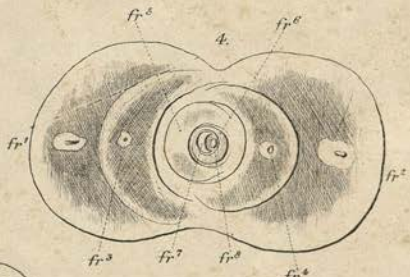
W. Hofmeister, del. Pullen West, sc.

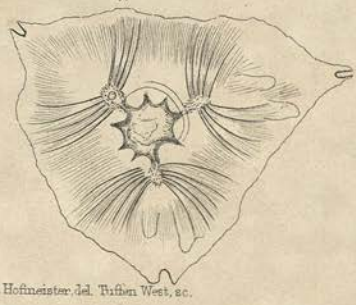
W. West, imp.

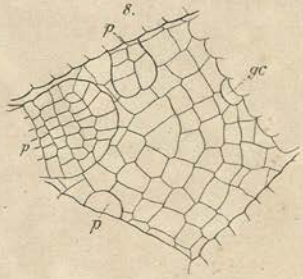






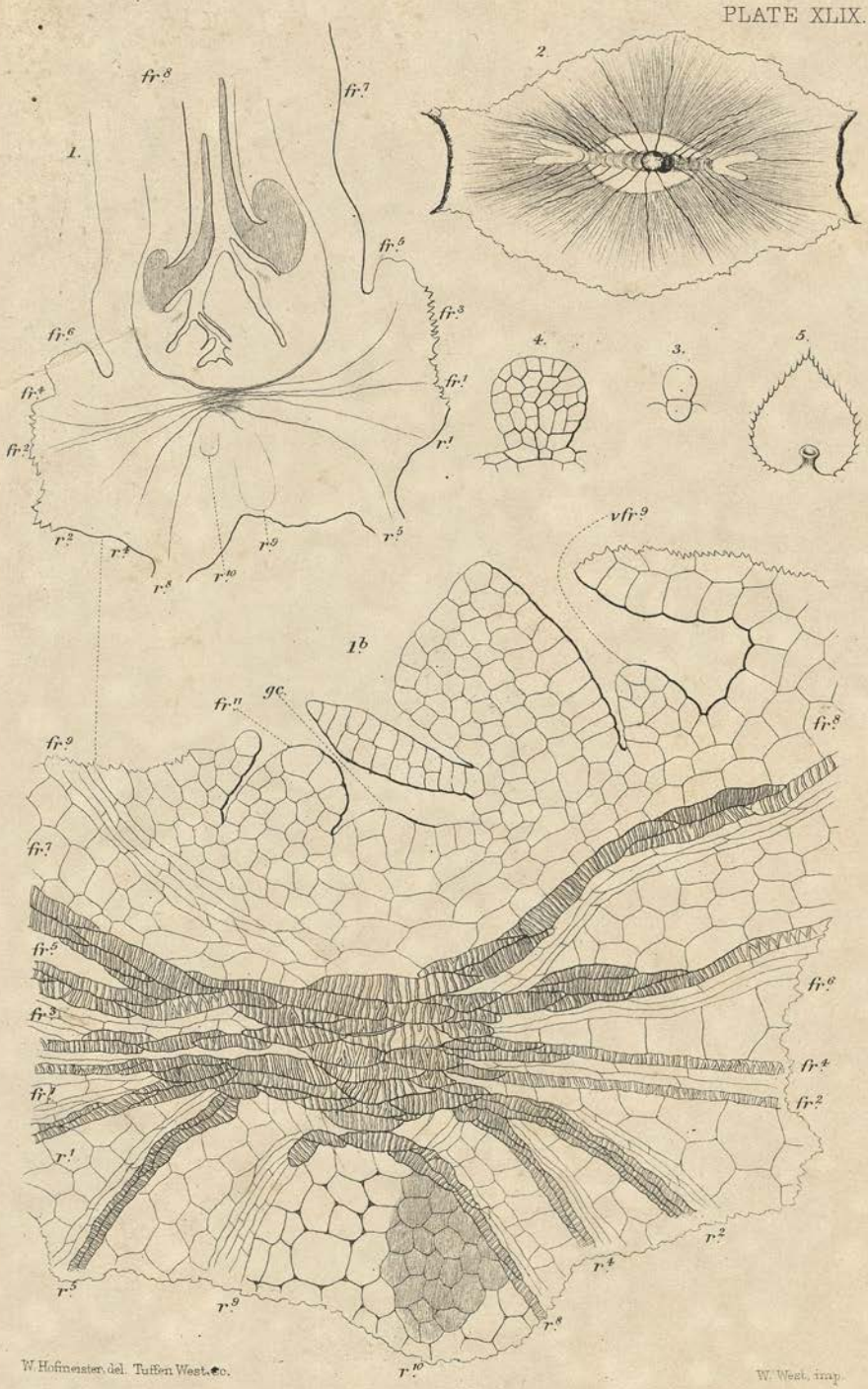






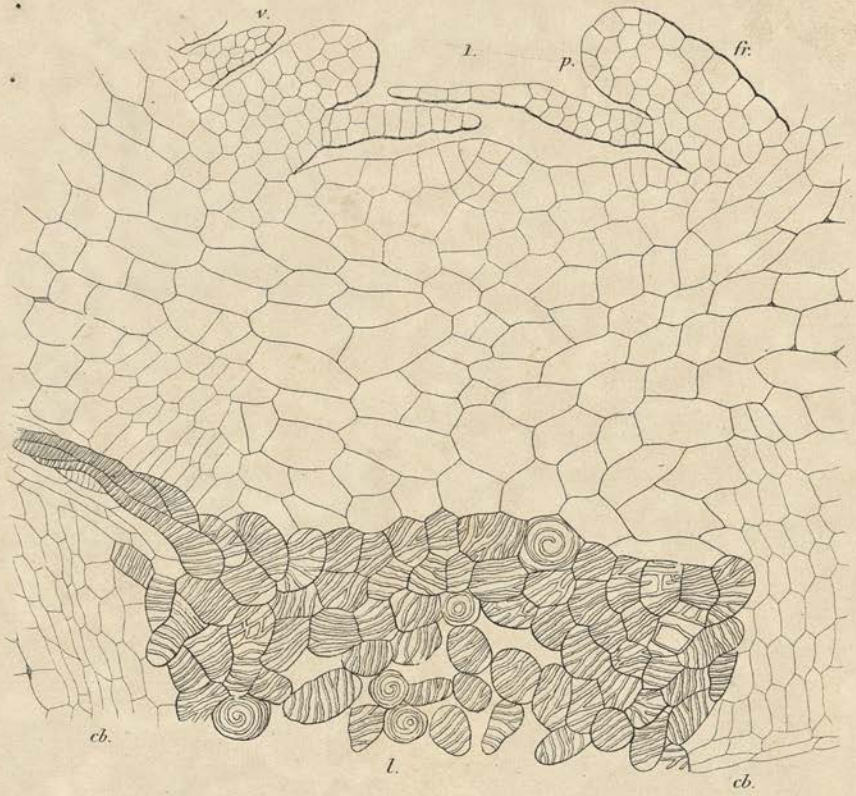
W. Hofmeister, del. Tuffen West, sc.

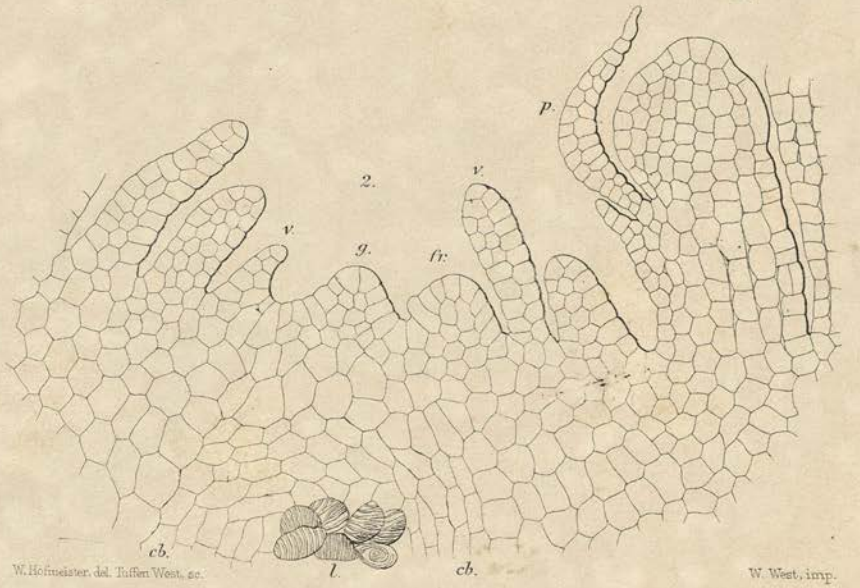
W. West, imp.



W. Hofmeister del. Tuffen West sc.

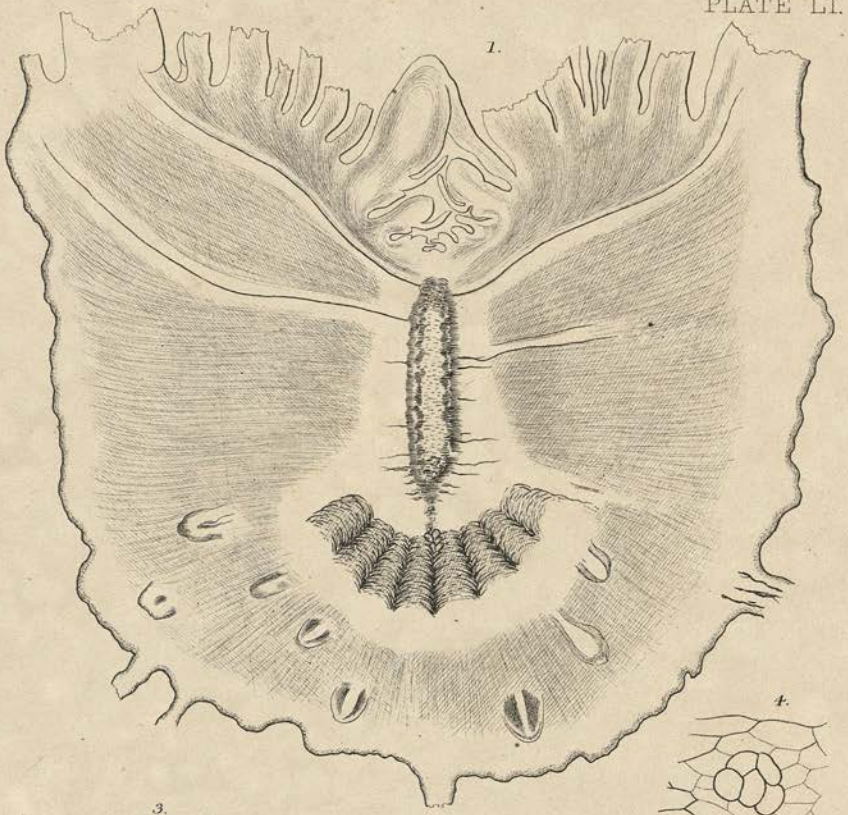
W. West, imp.

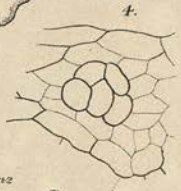


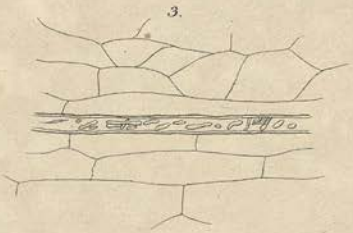


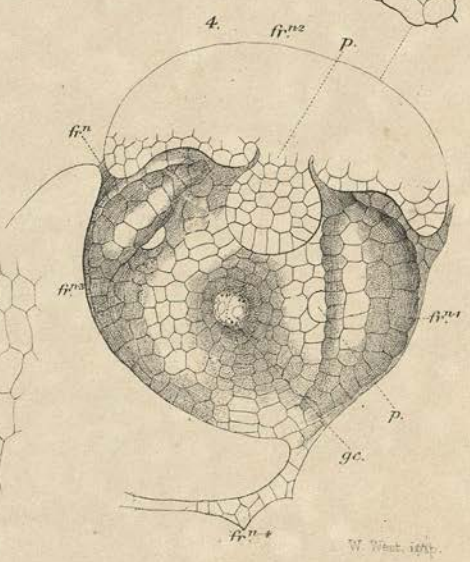
W. Hofmeister, del. Tuffen West, sc.
W. West, imp.

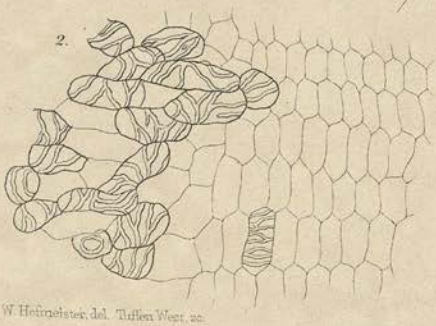
PLATE LI.







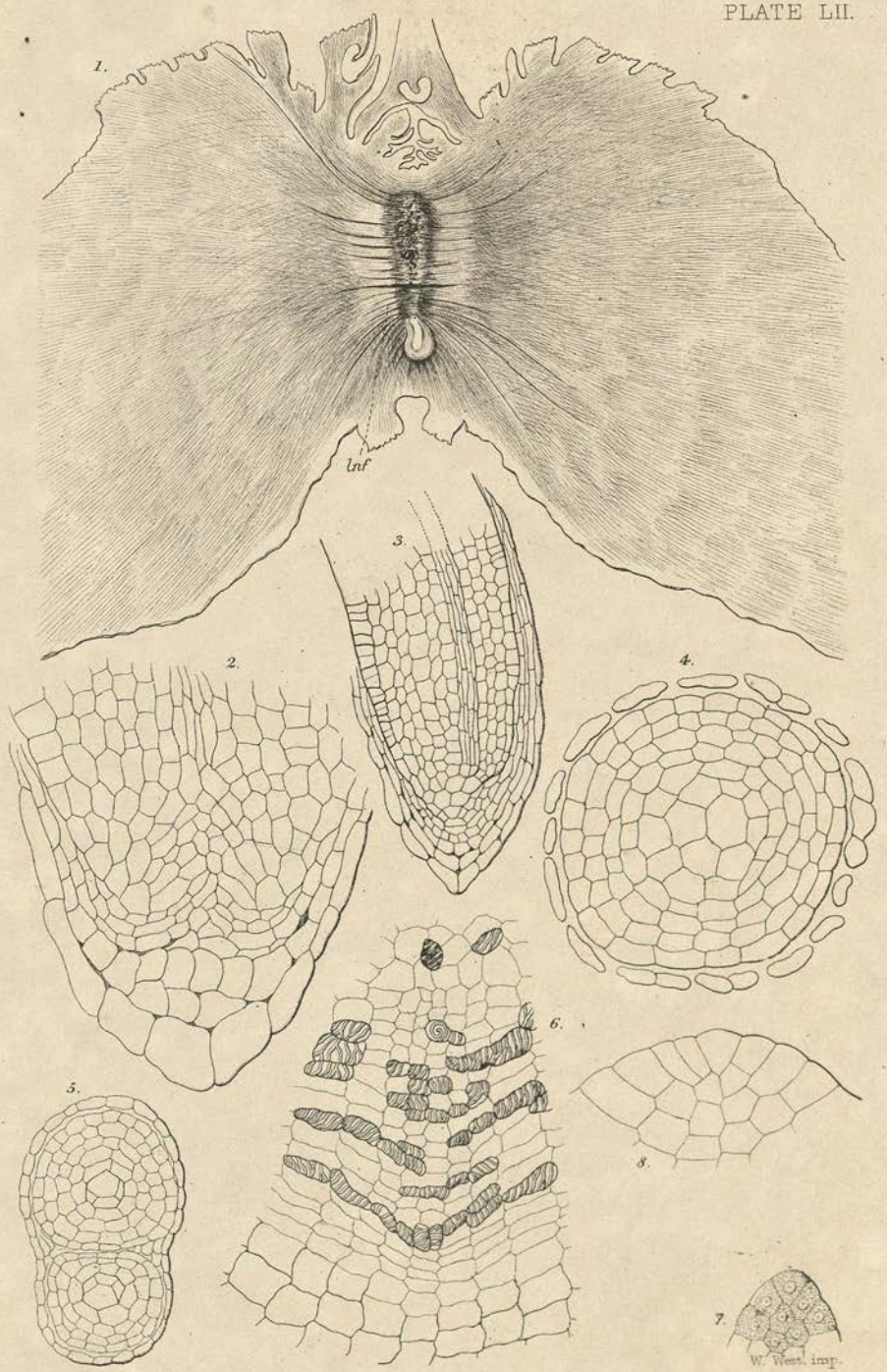




W. Hofmeister, del. Tuffen West, sc.

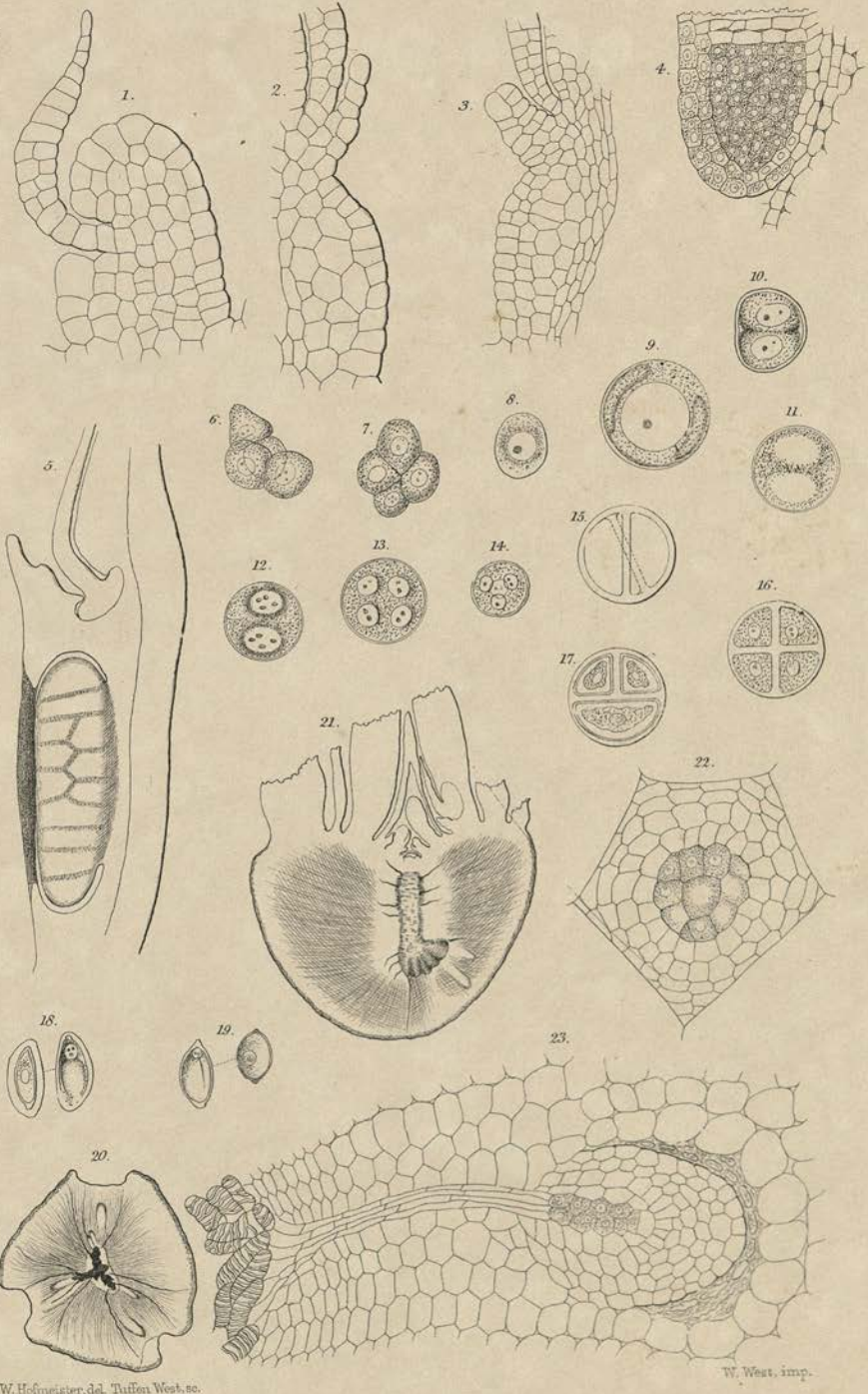
W. West, imp.

PLATE LII.



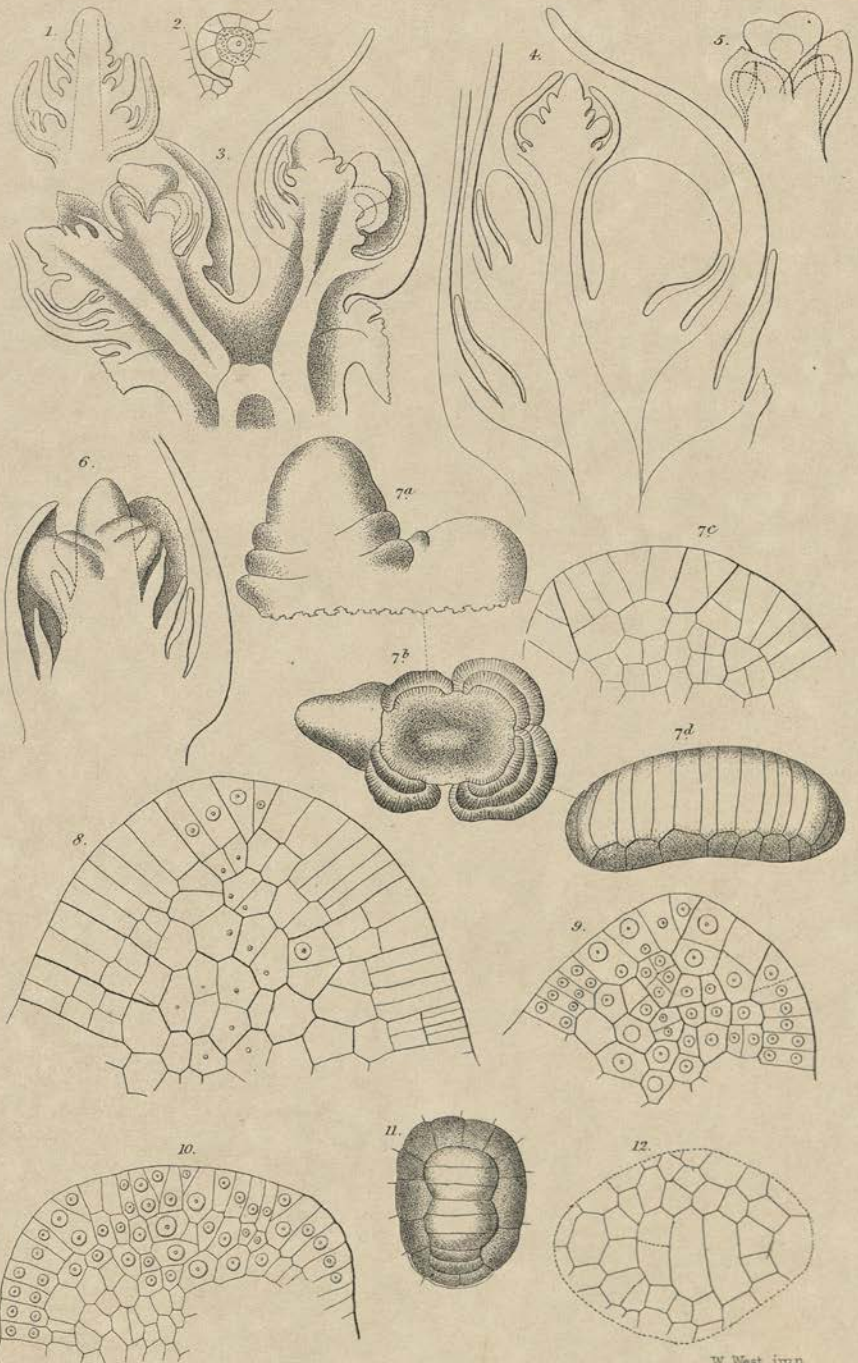
W. Hofmeister del. Tuffen West. sc.

W. West. imp.



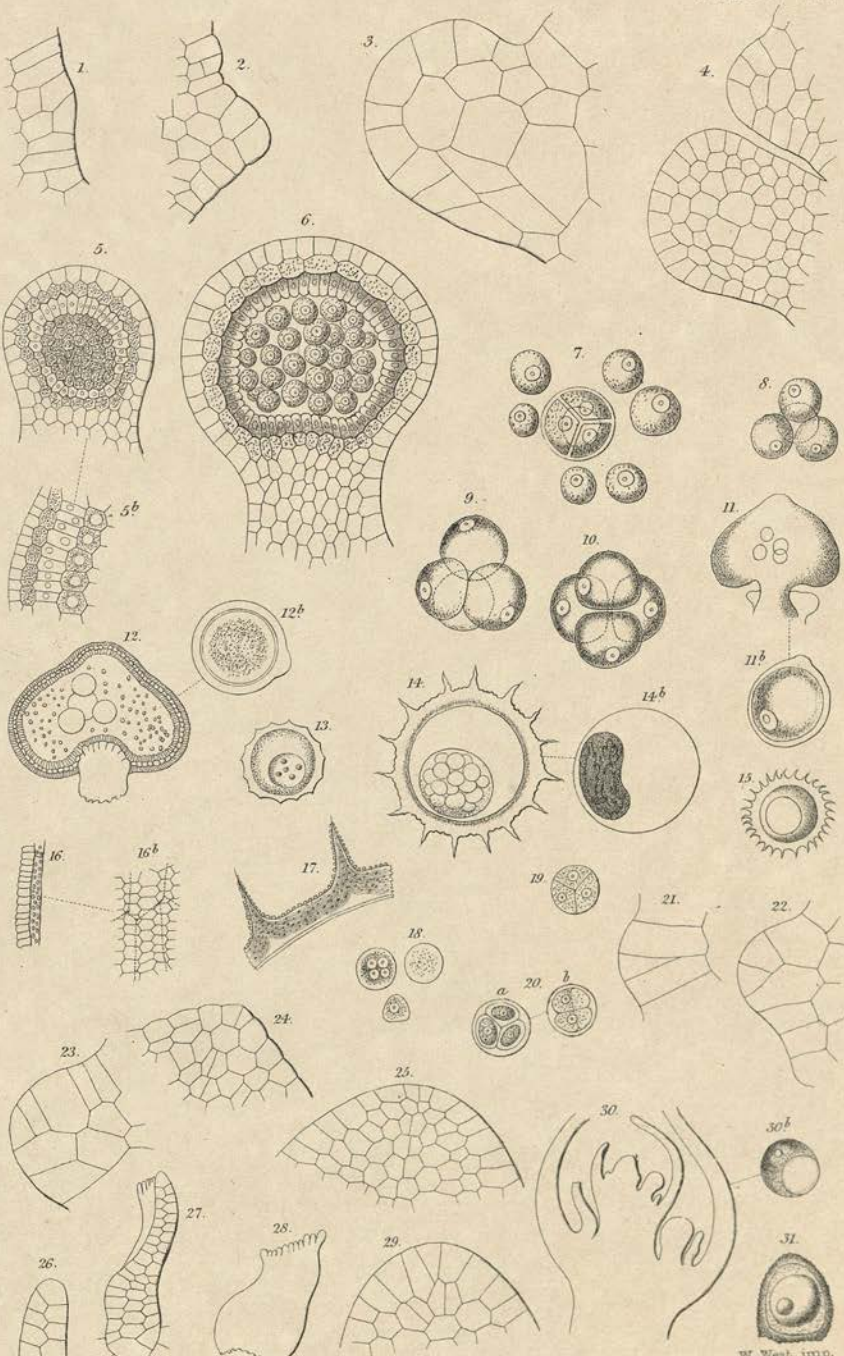
W. Hofmeister, del. Tuffen West, sc.

W. West, imp.



W. Hofmeister, del. Tuffen West, sc.

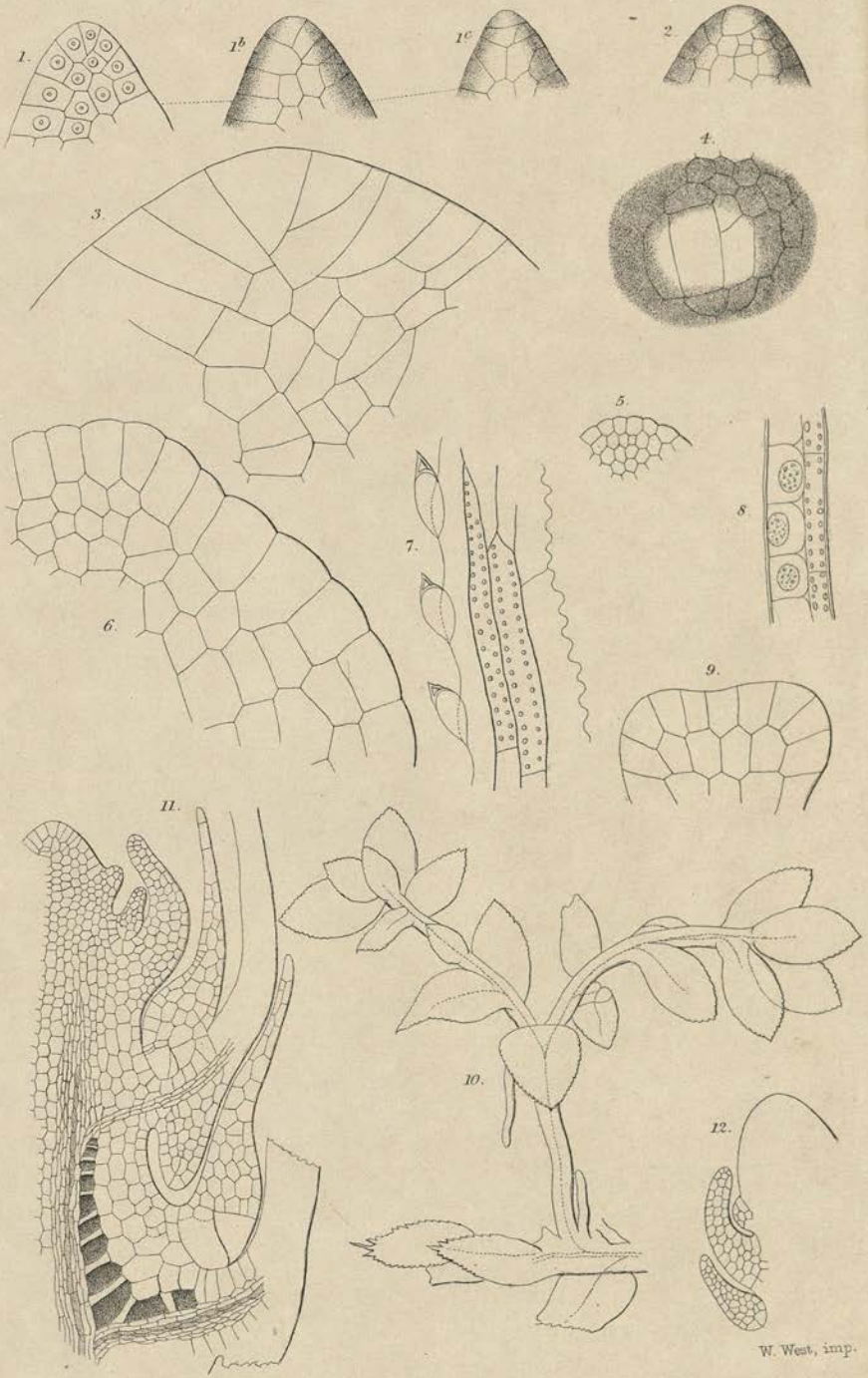
W. West, imp.



W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

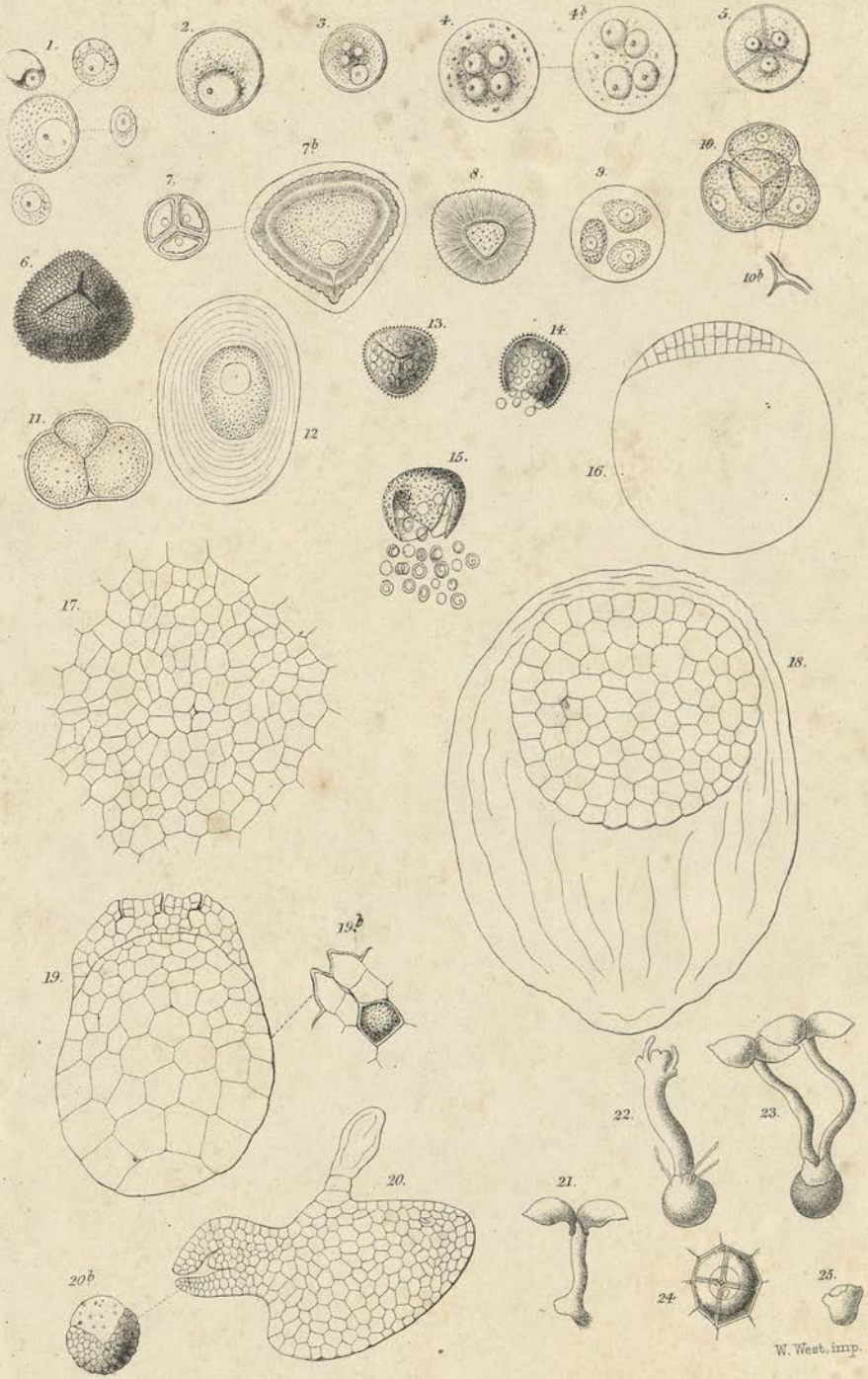
PLATE LVI.



W. Hofmeister del. Tuffen West, sc.

W. West, imp.

PLATE LVII.



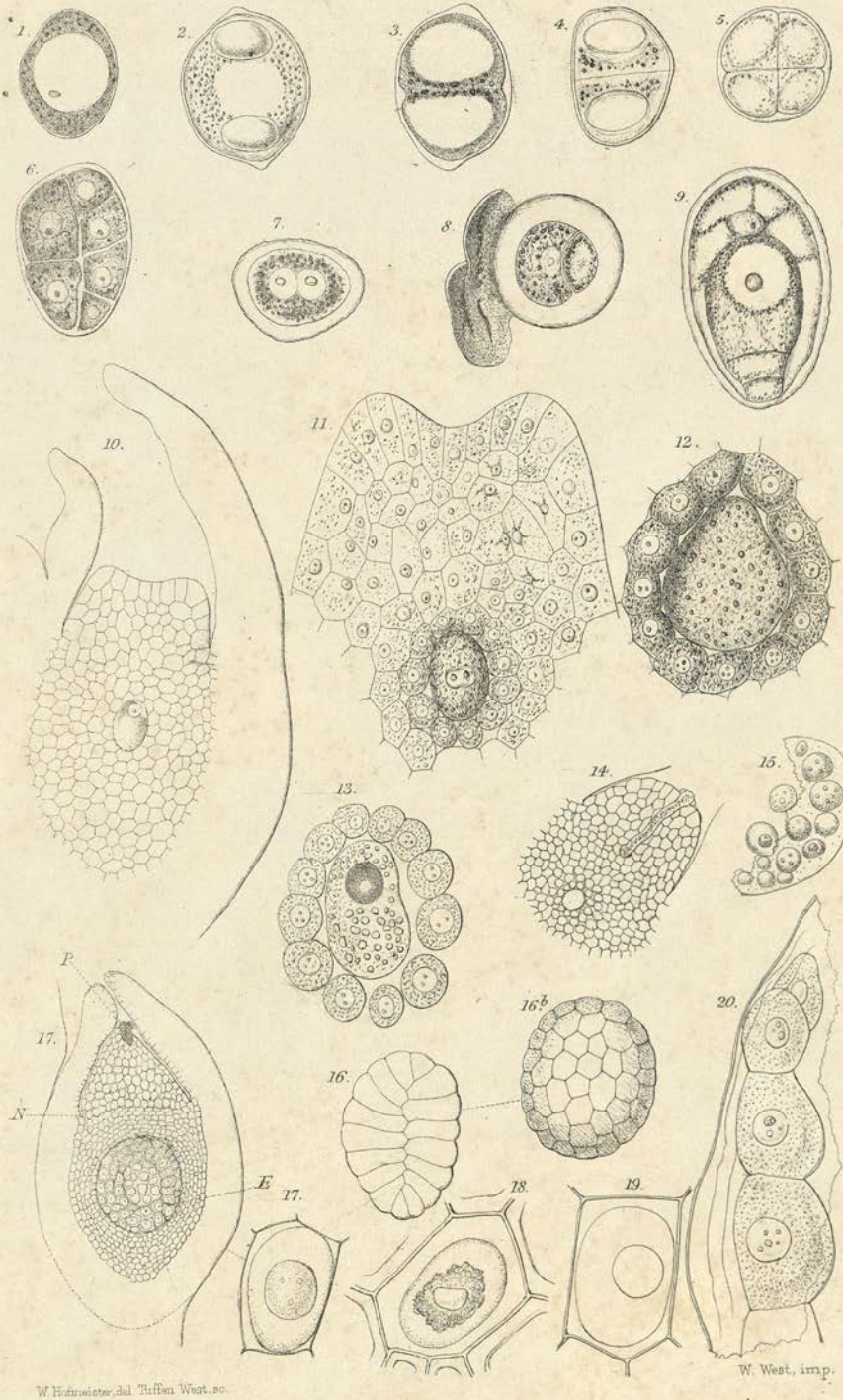
W. Hofmeister del. Tuffen West sc.

W. West, imp.

W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

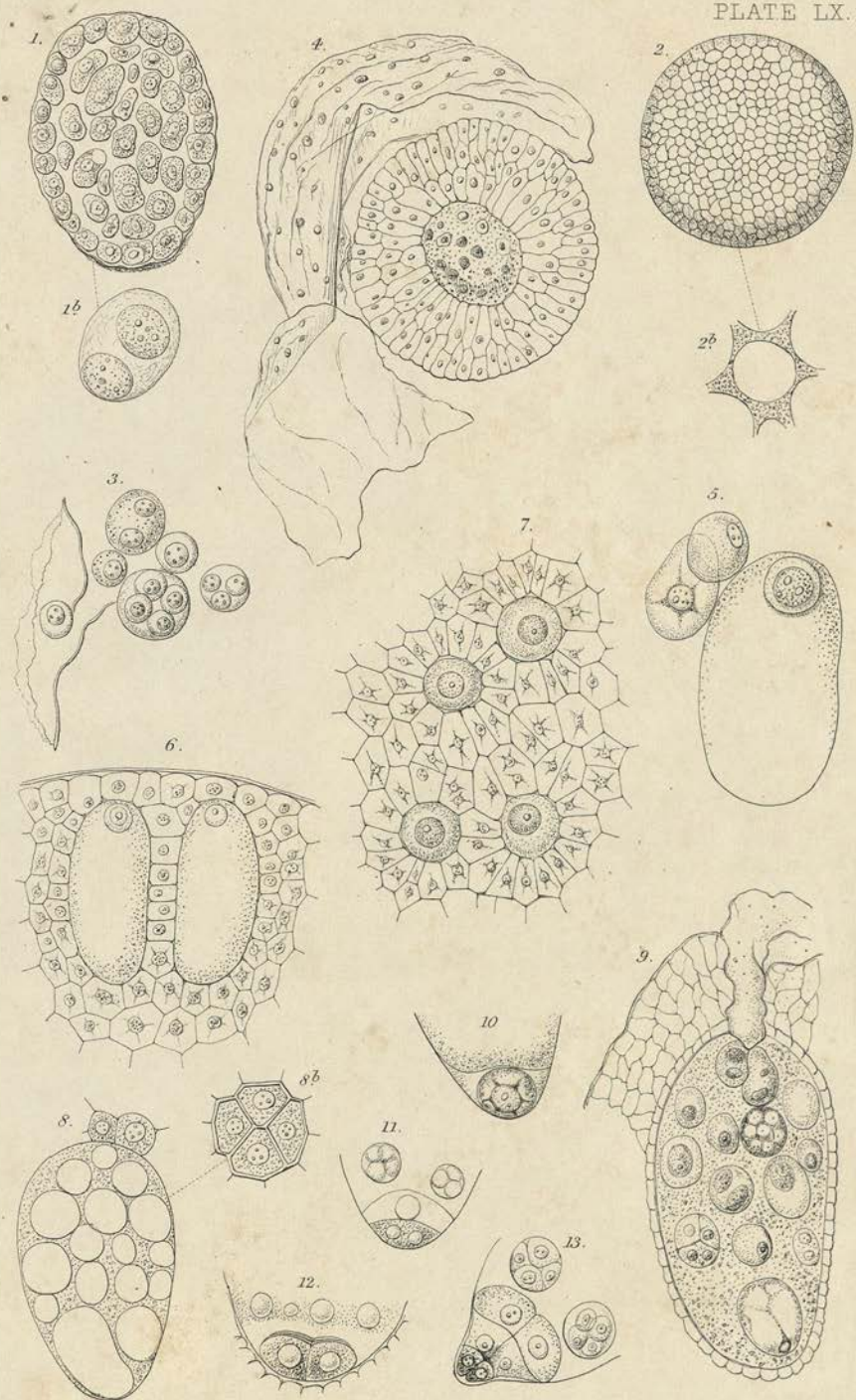
PLATE LIX.



W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

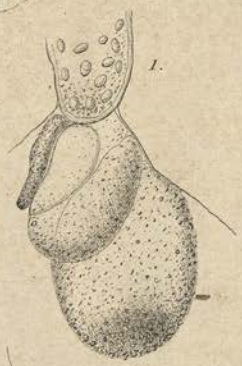
PLATE LX.



W. Hofmeister, del. Tuffen West, sc.

W. West, imp.

PLATE LXI.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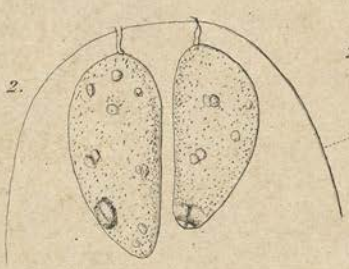
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2b

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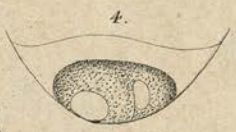
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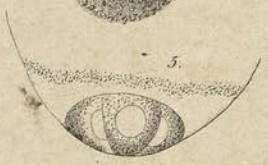
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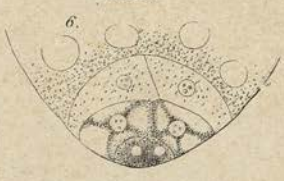
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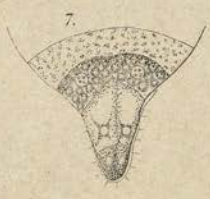
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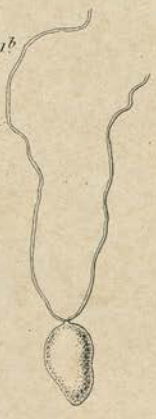
8.

9.

10.


11b

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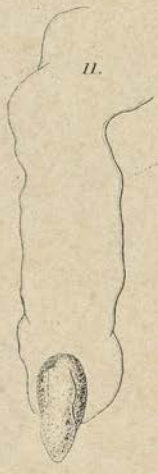
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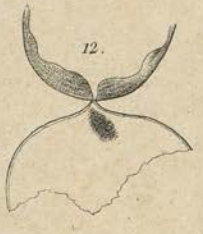

12.

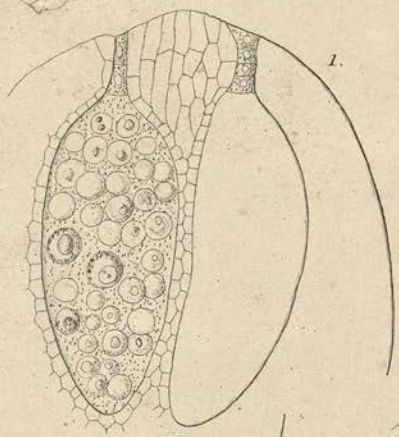
13.

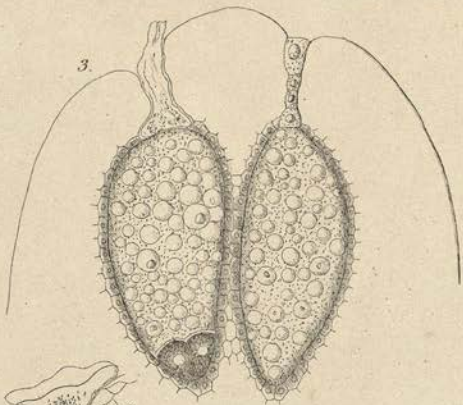
14.

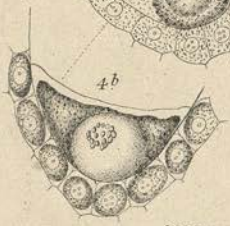
W. West, imp.

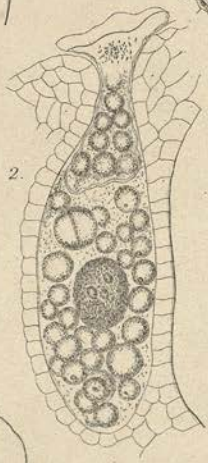
W. Hofmeister, del. Tuffen West, ad.

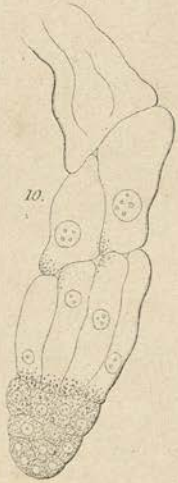
PLATE LXII.

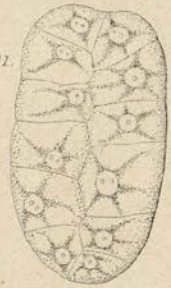








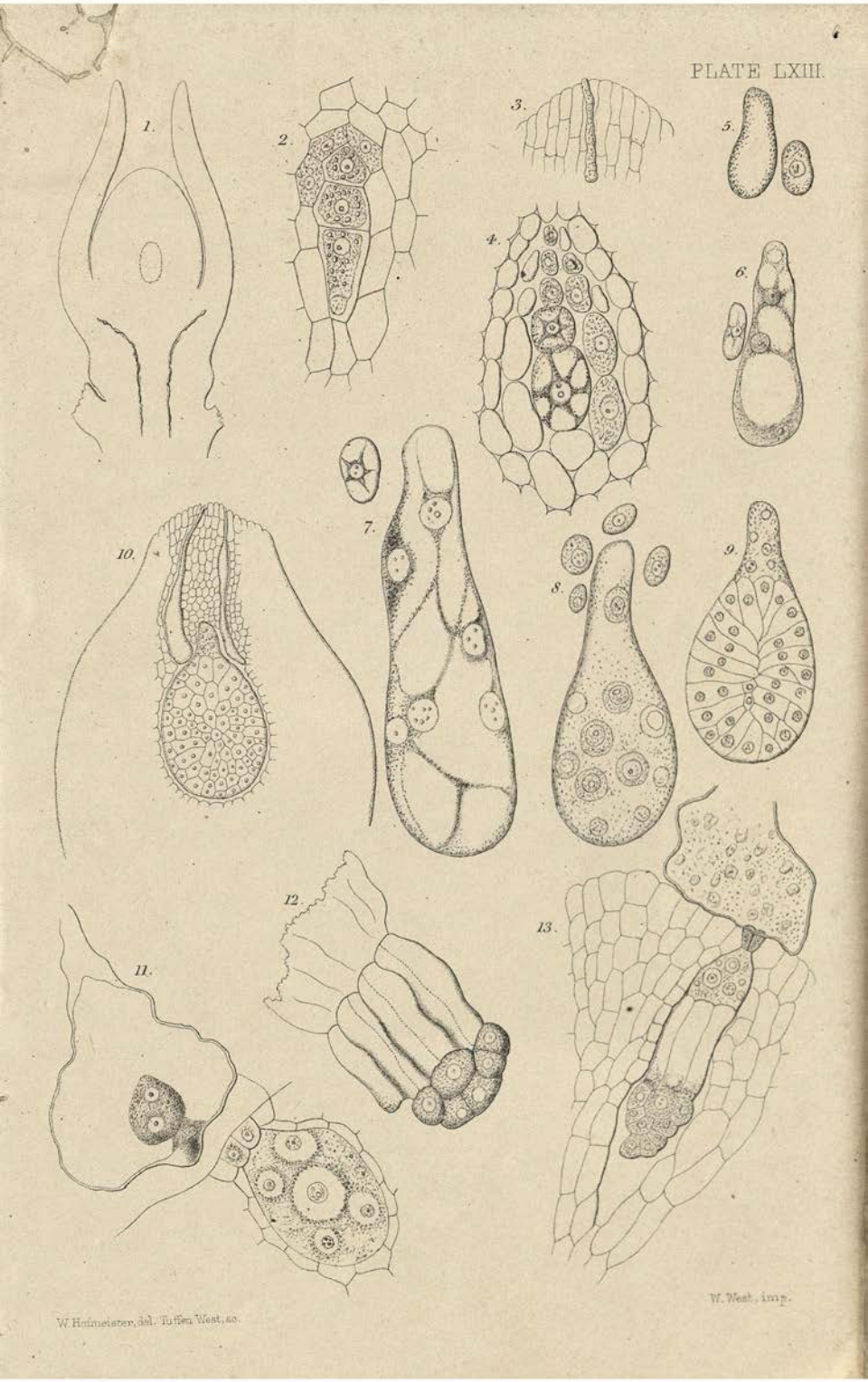




W. Hofmeister, del. Tuffen West, sc.

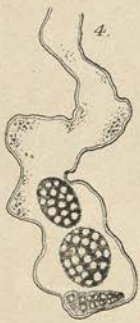
W. West, imp.

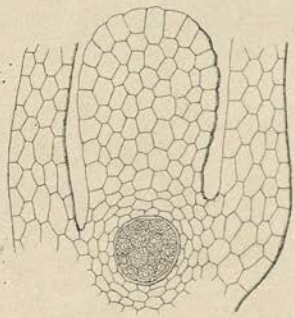
PLATE LXIII.



W. Hofmeister, del. Tuffen West, sc.

W. West, imp.





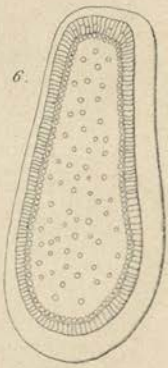


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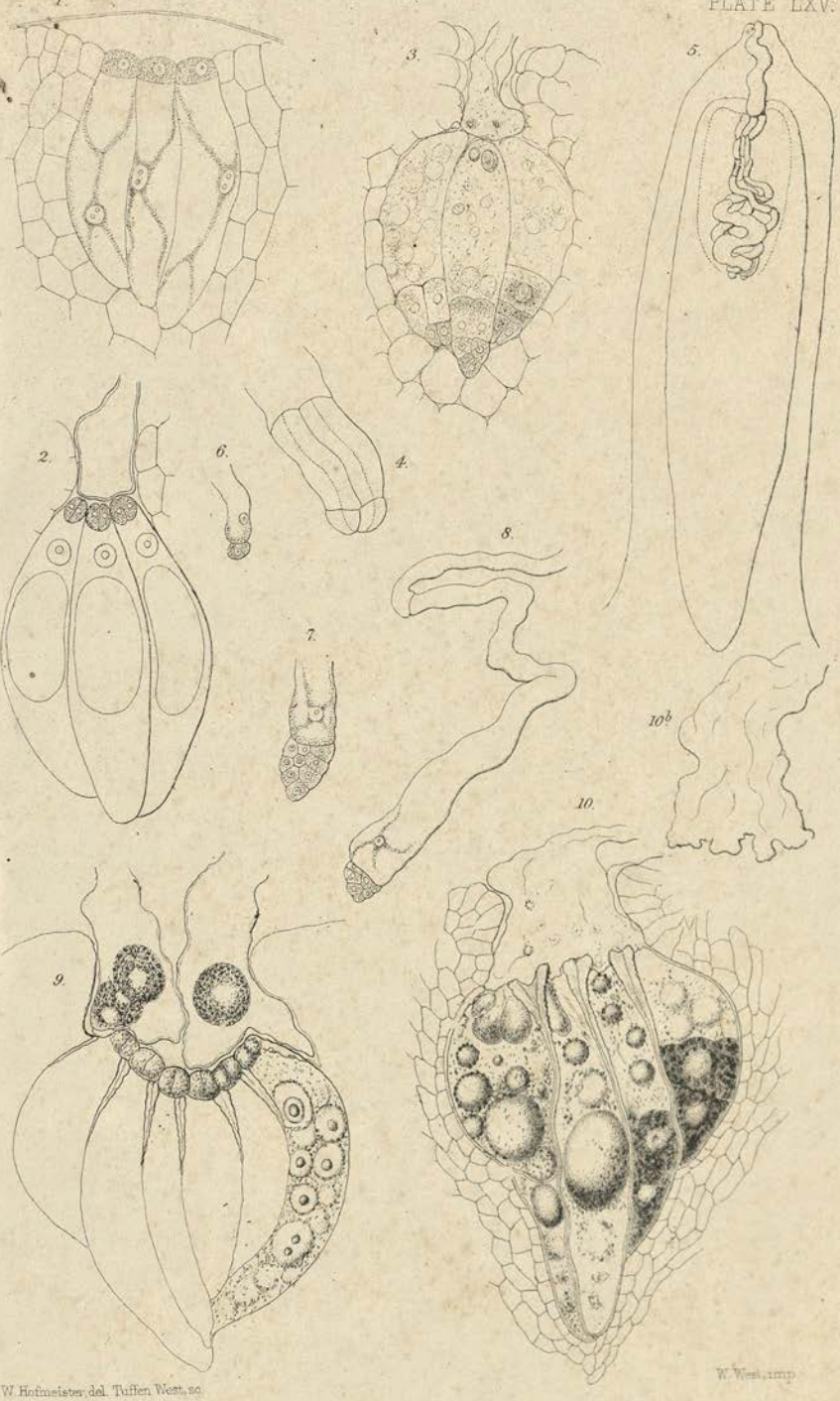
PLATE LXV.



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